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Let there be pike!

Effects of fishing on the dynamics of pike (*Esox lucius*) populations

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ACADEMIC DISSERTATION

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Hauki on kala.

-a Finnish proverb

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A LIST OF PUBLICATIONS

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AUTHOR'S CONTRIBUTION

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ABSTRACT

Pike (*Esox lucius*) is a keystone species and top predator, which has an important role in lake ecosystems and in recreational fishing. Recreational fishing is strongly size-selective on large fish, which can have detrimental effects on fish populations. The aim of this thesis was to study the ecologically sustainable recreational fishing of pike, and the importance of large pike to population resilience and ecosystem balance.

The field studies of this thesis were conducted in four small and almost pristine forest lakes in southern Finland in years 2006-2013. Two different size-selective fishing procedure for pike were applied; minimum length limit -regulation (MLL) of 40 cm and harvestable slot length limit -regulation (HSL) of 40-64.9 cm. During the study, fishing-induced responses in pike population abundance, demographics, production and consumption, as well as reflection of these changes in prey fish populations were monitored. Changes of pike diet and trophic position were studied by stomach content and stable isotope analysis. Also the relation of size-dependent maternal and juvenile characteristics was examined.

The main finding of this thesis is that HSL is capable to maintain viable pike populations. HSL preserved population density, biomass and diverse size-structure, as well as high pike production and consumption by diverse sized pike. By MLL those features were greatly degenerated. By protecting large fish, HSL is able to preserve the productivity of the fish population, because fishing mortality is compensated by increased recruitment and growth. In addition, HSL maintained stability of pike consumption, which enables a strong piscivore effect on the ecosystem. Based on the high quality and amount of reproductive products of large females, they are important for the reproduction of pike populations, which should be considered in fisheries management.

1. INTRODUCTION

1.1. The significance of pike in the ecosystem

Predatory fish are essential to the balance of entire aquatic ecosystems, as they have a stabilizing effect on trophic structure (Kuparinen et al. 2016). Pike (*Esox lucius*) is a keystone species and top predator in lake ecosystems. It is a fast-growing, large and abundant piscivore, which has great adaptability to different environments, as underlined by its

circumpolar native distribution in the northern hemisphere thorough Europe, Asia and North America (Raat 1988, Craig 2006). Pike is a freshwater species, but it is also present in brackish water e.g. in the Baltic Sea, where salinity and proximity of spawning grounds regulate its distribution (Lehtonen et al. 2009, Jacobsen et al. 2017). Pike is important in terms of top-down regulation of the trophic structure of an ecosystem, and it can control the abundance and structure of prey fish populations directly by predation (Raat 1988, Findlay et al. 2005), but also indirectly through predation threat (Persson et al. 1996, Skov et al. 2007, Estlander and Nurminen 2014). Due to its large gape size, pike is able to ingest large-sized prey (Hart & Hamrin 1988, Nilsson & Brönmark 2000). As a visually oriented ambush predator, pike can wait for prey for long periods, and then suddenly burst on passing prey (Raat 1988, Craig 1996). Pike favor structured habitat (e.g. vegetation, rocks, etc.), as they offer hiding place for ambushing, and shelter from other predators, such as piscivorous birds or larger pike (Bry 1996).

Pike is renowned from cannibalism, which strongly affects its population dynamics by density-dependent mechanisms (Raat, 1988, Craig 1996). Cannibalism has a particularly important role in high pike densities, and it decreases the intraspecific competition and population fluctuations (Anderson et al. 2007). Cannibalism is also common in environments with low abundance of other prey species and among young pike (Craig 1996). Besides cannibalism, pike population dynamics are strongly modified by inter- and intracohort competition for food and territory, in which large-sized pike usually have an advantage (Persson et al. 1996). For cannibalistic and kleptoparasitic species, such as pike, the size-related competition advantage is particularly high, as larger pike may outcompete their smaller siblings by cannibalizing them or by stealing their prey (Anderson et al. 2007). Especially in early stage of life, size has a high importance, as diet shift from zooplankton to invertebrates and fish is dependent on pike size, and the change to larger and more energy-rich prey has a positive impact on growth (Frost 1954, Grimm & Klinge 1996). In favorable environments, the advantage may be cumulative throughout an individual's lifetime, eventually resulting in the presence of large, "trophy" pike in a population. However, high pike densities in relation to food resources, unfavorable environment and the absence of large-sized prey may overrule this advantage, leading to a high population density of small pike (Margenau et al. 1998, **I**, **II**).

1.2. Humic lakes as habitats for pike

Humic lakes are common in the native distribution of pike in the boreal zone (Kortelainen 1999), and thus they represent well the natural environment for pike. Humic lakes have high concentration of dissolved organic compounds, principally humic substances. These lakes are characterized by highly colored water and low euphotic depth, as well as strong temperature and oxygen stratification during summer and winter stagnation (Kortelainen 1999, Rask et al. 1999). A large part of the production in small humic lakes is derived from the littoral zone, because pelagic production is more limited due to the small pelagic volume and low euphotic depth (Rask et al.1999). In humic lakes, macrophyte cover is often limited near to the shoreline, since high terrestrial dissolved organic carbon (t-DOC) suppress pelagic and benthic reproduction (Rahel 1984, Karlsson et al. 2009, Vadeboncoeur et al. 2008). Also coarse woody habitat (e.g. fallen trees) increases the importance of the littoral zone in humic lakes, as this offers microhabitats for macroinvertebrates and fish (Harmon et al. 1986, Benke & Wallace 2003). These circumstances have profound effects on species dynamics and abundance. As humic lakes are generally nutrient-poor, growth of fish and consequently production is often low (Rask & Arvola 1985, Rask et al. 2009, Pierce & Tomcko 2003), and consequently a high degree of inter-and intraspecific competition for resources is common (Persson 1990, Linløkken & Hesthagen 2011).

As a visually oriented predator, low visibility of humic lakes limits the predation efficiency of pike (Jönsson et al. 2013). Foraging of pike in humic lakes is further restricted by the low number of prey species, of which perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and other pike are the most common in Finland (Rask et al. 1999). High surface temperature and thin oxygenated layer have negative impacts on pike growth (Margenau et al. 1998). A deep oxygenated layer is especially crucial for growth of large pike, as they have higher oxygen demand and lower optimum temperature than smaller individuals (Casselman 1978, Diana 1996, Pierce et al. 2013). Also limited availability of suitably sized prey fish may depress pike growth (Rask et al. 1999). Invertivory in these conditions is likely a result of limited per capita availability of more energy-rich resources (Chapman et al. 1989, Vander Zanden & Vadeboncoeur 2002, Venturelli & Tonn 2006), combined with competition pressure and predation threat. Growth rate is greater in young fish, because no energy is allocated to production of reproductive products (Diana 1996). Growth is usually strongly density-dependent, and the fastest growth is typically achieved in low population densities,

as the competition on food and habitats decreases (Casselman & Lewis 1996, Margenau et al. 1998).

1.3 The significance of large individuals

Traditional fisheries regulations encourage harvesting of large and old fish, which usually are the least productive part of the population in terms of biomass yields (Walters & Martell 2004, Gwinn et al. 2015). The rationale behind this positive size-selectiveness is to increase fisheries yield-per-recruit by releasing resources for growth for the smaller and more productive part of population (Birkeland & Dayton 2005, Gwinn et al. 2015). However, removal of large fish can have detrimental effects on fish populations. Female fish are larger than males, and they have higher catchability due to their higher activity, which stems from their higher energy demands (Lewin et al. 2006.) In pike (Craig 1996) and many other large, piscivorous fishes (e.g. Berkeley et al. 2004b), large females are essential to the vitality of a population, as they have higher fecundity than smaller females. The importance of large females is further amplified by the maternal effect, which is a female size and fitness-related influence on offspring phenotype (Bernardo 1996). Large and fit females usually have better capability to invest energy on reproduction, which is expressed as heavier eggs or larger larvae (Wright & Shoesmith 1988, Billard 1996, Ojanguren et al. 1996), but the quality of eggs and larvae may also be mediated by female age (Berkeley et al. 2004a, Kamler 2005, **IV**). High dry weight is related to higher energy content of juveniles and, consequently, it increases the starvation resistance in early life (Berkeley et al. 2004a, Kamler 2005, Marshall et al. 2008, **IV**). In addition, energy investment on larvae promotes larval growth, decreases vulnerability to predation (Perez and Munch 2010) and enhances the capability to use various prey items (Mehner et al. 1998). According to some studies, the maternal effect occurs also in pike (Nikolsky 1974, Arlinghaus et al. 2010, **IV**), but in other studies the effect was not found or the results were contradictory (Wright & Shoesmith 1988, Murry et al. 2008), and the importance of the maternal effect in the wild is not yet unraveled completely (Pagel et al. 2015).

Loss of large females also increases the risk of genetic shift towards smaller size and earlier reproduction (Van Wijk et al. 2013, Kokkonen et al. 2016). Compared to terrestrial animals, the natural selection for larger size is particularly strong in fish. Perez & Munch (2010) reviewed 40 studies, and 77 % of analyzed selection differentials favored larger size in early life of fish, and selection pressure was five times stronger

than in terrestrial animals. However, in fisheries-induced selection pressure, the effect is opposite. In their 50 year study of pike in Lake Windermere, Edeline et al. (2007) reported strong selection towards decreased somatic growth and early reproduction under heavy exploitation, but this development was reversed after fishing decreased and the pike population recovered. As a result of size- and sex-selective exploitation, negative life-history changes, such as truncation of size and age distributions, and decreased size and age of maturity, have been perceived and observed in many exploited fresh- and brackish-water fish species including pikeperch (Kokkonen et al. 2015), perch (Pukk et al. 2013, Olin et al. 2017) and pike (Edeline et al. 2007, Pierce 2010, Carlson 2016). These impacts have been perceived in laboratory (Van Wijk et al. 2013, Uusi-Heikkilä et al. 2015), model-based (Post et al. 2003, Arlinghaus et al. 2009, Matsumura et al. 2011, Vainikka et al. 2017) and experimental studies in the wild (Mosindy et al. 1987, **I**, **II**). Taken together, management strategies should aim to protect, rather than target, reproductively valuable individuals, as suggested by Venturelli et al. (2010).

1.4. Fisheries management in recreational fisheries

Although fisheries-induced changes in population dynamics are a well known phenomenon in commercial fisheries, in recreational fishing these impacts not as well recognized (Post et al. 2002). In the industrialized societies angling dominates the use of fish stocks in most freshwater and in some coastal areas (Welcomme 2001, Arlinghaus et al. 2002, Cooke & Cowx 2006, Lewin et al. 2006). The population dynamics -based stock assessment, and harvest regulations, which is often used by commercial fisheries to optimize harvest (Walters & Martell 2004), are rarely used in recreational fisheries (Post et al. 2002, Allan et al. 2005, FAO 2012, Post 2002, Post 2013). Stock assessment in recreational fisheries is inherently difficult, due to an absence of reliable statistics, diversity of participants and dispersed landings (Arlinghaus et al. 2002, Allan et al. 2005). Stock assessment is also expensive and requires time, specialized equipment and personnel (FAO 2012). Population dynamics of exploited species may also be complicated, and density-dependent responses in growth, survival, reproduction and movement of fish are difficult to predict for specific populations (Rose et al. 2001). Fisheries regulations by recreational fisheries is thus usually assessed by indirect and easy-to-apply approaches, in which relatively low amount of involvement by fisheries stakeholders and anglers is required (Post 2013, Gwinn et al. 2015).

Pike is one of the most popular species in recreational fishing in freshwater ecosystems (Paukert et al. 2001, Arlinghaus & Mehner 2004). The popularity of pike as a gamefish is explained by its large size and ferocious fighting when hooked. Pike has high catchability due to its abundance and aggressive feeding (Pierce et al. 1995, Paukert et al. 2001), and trophy-sized individuals are also highly valued by specialized anglers (Arlinghaus et al. 2007). On the other hand, some fishermen don't appreciate pike at all, and kill and abandon their catch (Paukert et al. 2001). As a result of these factors, the pike is very vulnerable to fishing (Mosindy et al. 1987, Pierce et al. 1995, Pierce & Tomcko 2003). In their study in seven small north-central Minnesota lakes, Pierce et al. (1995) reported as high as 0.46 mortality rate for pike larger than 50 cm. In the experimental pike fishery, Mosindy et al. (1987) observed that even moderate fishing effort removed annually 50 % of adult pike production. Consequently, several popular recreational fisheries have failed to produce large trophy fish for recreational fishing (Pierce 2010, Oele et al. 2016). Therefore, sustainable management is needed to improve deteriorated pike populations, and to maintain long-term sustainability of viable pike populations (Arlinghaus et al. 2010, Pierce 2010, Carlson 2016).

In order to overcome the negative effects of size-selective harvest, several methods for fisheries management have been developed. Length-based regulation strategies have been commonly applied (Paukert et al. 2001, Arlinghaus et al. 2002), of which the most traditional is the minimum length limit –regulation (henceforth MLL) in recreational fishing (Arlinghaus et al. 2010, Pierce 2010, Gwinn et al. 2015). However, popular recreational fisheries with MLL and high exploitation rates have constantly failed to maintain adequate numbers of individuals substantially larger than the value of the MLL (Pierce 2010, Oele et al. 2016), which has led to negative responses as previously described. Alternative length-based management strategies have also been developed, such as maximum length limit, in which fish larger than the threshold length are conserved, as well as protected slot length limit, which allows harvest of large and small individuals, but intermediate-sized fish are conserved (Paukert et al. 2001, Pierce 2010, Gwinn et al. 2015). According to recent knowledge, the most reasonable length-based management tool would be harvestable slot length limit – regulation (henceforth HSL). In this type of management, small individuals, which have not achieved their growth or reproduction potential, and large fish, which are considered valuable for their importance to ecosystem and reproduction potential, or for recreational

fishing, are protected (Arlinghaus et al. 2010, Matsumura et al. 2011, Carlson 2016).

Length-based regulations can also be used with other management tools to control fishing mortality. These tools may include spatial or temporal restrictions, (e.g. at spawning areas or times), restricted access to fisheries by the number of licenses, by setting up bag limits for anglers (Paukert et al. 2001, Cooke & Cowx 2006), or mandatory or voluntary catch and release (C&R) (Arlinghaus et al. 2007, Stålhammar et al. 2014). Pike fisheries can be managed by C&R –based regulation, as pike is relatively resistant to post-release mortality and sublethal effects (Tomcko 1997, Arlinghaus et al. 2008, Klefoth et al. 2008, Stålhammar et al. 2014). Nevertheless, some degree of mortality and sublethal effects, like physical injury and alterations in growth and behavior are likely to occur (Klefoth et al. 2008, Stålhammar et al. 2014). The acceptability of catch-and-release has also been debated, due to the harm inflicted on an animal for the purpose of leisure (Arlinghaus et al. 2014). In many countries, the concept of “selective harvest” is considered more acceptable than “pure” catch and release fishing (Arlinghaus et al. 2007, Arlinghaus et al. 2014).

Although in commercial fishing a conflict exists between maximizing harvests and minimizing ecosystem effects (Walters & Martell 2004), in modern recreational fishing this is not necessarily the case. Modern-day recreational fisheries are increasingly motivated by leisure-related factors (Arlinghaus et al. 2010, Gwinn et al. 2015, Carlson 2016), and thus possible reduction in yields can be considered as an acceptable trade-off between consumptive motives and the preservation of large pike for recreational fishing or conservational purposes (Pierce 2010, Matsumura et al. 2011, Gwinn et al. 2013, Carlson 2016). Nevertheless, fishing-mediated life-history-related changes are likely to occur to some extent by any length-limit-based regulation (Matsumura et al. 2011, Vainikka et al. 2017).

2. RESEARCH OBJECTIVES AND STRUCTURE OF THESIS

The general aim of this thesis was to study the ecologically sustainable recreational use of pike populations. More specifically, I evaluated how MLL- and HSL-regulated fishing induced changes in pike population parameters including abundance, and size, age and sex structure. In particular, I focused on the importance of large pike individuals to population resilience and ecosystem balance. I explored whether the maternal traits (size, age and growth rate) were related to the juvenile

characteristics (size and starvation resistance). I also studied how the fishing-induced demographic changes affected the production and consumption of pike populations and how these changes were reflected in prey fish populations.

The findings of this thesis have high practical value, as they give guidelines for sustainable length-based management for recreational pike fisheries. The material for this thesis was collected from long-term experimental fishing of pike populations in natural lakes, as part of the KESKALA project (2005-2014). Also laboratory experiments and applied models are based on data from the same well-studied populations.

The effect of fishing on pike density, biomass and sex-, size-, and age-structure are evaluated in article **I**, and responses in growth, production and consumption of prey fish in article **II**. Ecosystem effects of fishing are further studied in article **III**, in which fishing-mediated change in diet and trophic position for all size of pike was monitored. The effects of fishery-mediated maternal effect on offspring quality and survival are presented in article **IV**. The structure of the thesis is presented in following diagram (Fig. 1):

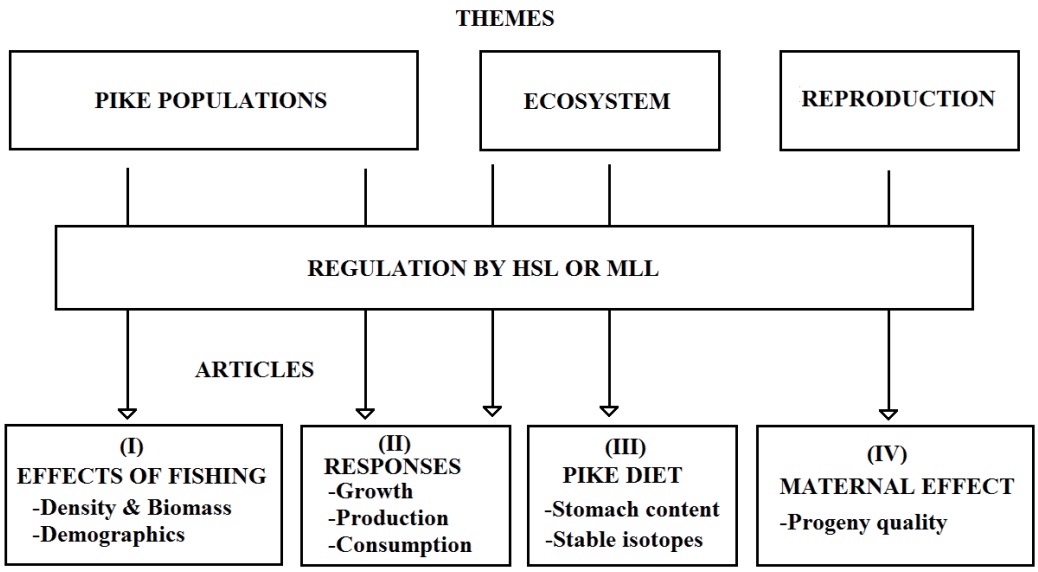

Figure 1. Schematic diagram of themes of the thesis.

3. MATERIAL AND METHODS

3.1. Study area

The study was conducted in southern Finland in Evo district, Hämeenlinna (61°13´N, 25°12´E) in four small (2.1-13.8 ha), close-to-pristine forest lakes during years 2006–2013 (Table 1). The lakes are relatively shallow (mean depth 2.2-6.1, oligo-mesotrophic (TP 7-29 µg l^{-1}), and colored by humic substances (water color 130-340 mg Pt l^{-1}) with relatively low Secchi depth (0.65-1.5 m). Lakes are not subjected to agricultural or industrial pollution, and they are reserved for research use only, i.e. any other fishing than for research is prohibited. Strong temperature stratification and subsequent hypoxic hypolimnion occur during summer and winter except in Haarajärvi, where the hypolimnion is well oxygenated through the year (Olin et al. 2010). The littoral vegetation zone in three of the study lakes is narrow (coverage 4%–15%), resulting in limited habitats for pike (**I**). The exception is Hokajärvi, where vegetation coverage is 80%. In all lakes, the dominant fish species are perch, roach and pike (Olin et al. 2010). Other species present in study lakes include bream (*Abramis brama*) and bleak (*Alburnus alburnus*) in Hokajärvi and Haukijärvi, burbot (*Lota lota*) in Haarajärvi, Haukijärvi and Hokajärvi, as well as small populations of introduced whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in Haarajärvi and tench (*Tinca tinca*) in Majajärvi.

*Table 1. Characteristics of the study lakes. * Horppila et al. 2010, **Estlander et al. 2009.*

Lake	Area * (ha)	Mean depth* (m)	Max depth* (m)	Water color * Pt l^{-1}	Secchi depth ** (m)	Total phosphorus** (µg l^{-1})
Haarajärvi (HSL)	13.8	6.1	12	150	1.2	13
Haukijärvi (HSL)	2.1	3.8	8	330	0.8	11
Hokajärvi (MLL)	8.4	2.2	6	130	1.5	7
Majajärvi (MLL)	3.4	4.6	12	340	0.65	29

3.2. Fish population monitoring

The fish populations in the lakes were monitored by two different methods during 2006-2013: mark and recapture and standard gillnet sampling. Pike population densities, biomasses and size structures in article **I** and **II** were estimated by a mark-recapture program with multigear sampling in order to minimize the effects of gear selectivity,

and to improve coverage and catch rates (Clement et al.2014). Pike were caught at spring spawning time (within 2-3 weeks after ice-break) in late April to early–mid-May with fyke nets and wire traps. Another pike marking and recapturing period was carried out in late August-early September, when intensive angling by rowboat and 1–2 anglers was focused on the littoral area of the study lakes. In that period, every lake was visited 1-2 times during dawn, midday and dusk. A variety of artificial lures, mainly of size 5–12 cm were applied in angling. For pike ≥ 30 cm (smaller individuals were not tagged due to assumed high post-release mortality), two types of individually coded tags were used: Carlin-tag in 2006 and Floy T-bar anchor tag in 2007–2013. Tags were inserted into muscle tissue at the base of the dorsal fin. All caught and released pike were marked by fin-clipping (right or left pelvic fin depending on the year) to control for tag loss, and to mark <30cm pike. Survival from tagging and handling was monitored for ca. 10 minutes in large tub of water. Severely injured individuals were immediately killed and included in the removal catch.

Population monitoring of perch in article **II** was conducted in spring with the same wire traps used for pike. Perch were marked by fin- clipping (tip of the left or right pelvic fin depending on the year (Horppila et al. 2010), measured for length (1 cm size classes) and sexed. The fishing was continued until the total density estimates (Schnabel multiple marking method, Seber 1982) reached <20% accuracy (95% CL) (**II**, Olin et al. 2016).

Standard gillnet fishing (CEN 2005) with Nordic multimesh gillnets (mesh size 5–55 mm) and stratified random sampling (Olin et al. 2010) was implemented annually in July–August to determine fish population assemblage in the study lakes. Of the gillnet catch, catch per unit effort by weight (g gillnet^{-1}), henceforth BPUE, was used as an index of perch and roach abundance (Olin et al. 2016) in article **II**.

3.3. Size-selective fishing procedures

In **I** and **II**, the impact of fishing (in which large individuals were either targeted or released) on the pike population and also other ecosystem parameters was studied. Two different size-selective harvesting procedures were conducted during 2008–2012 (**I**). The procedure MLL of 40 cm was implemented in two of the study lakes (Hokajärvi and Majajärvi), representing the “traditional” length-limit –based regulation, in which MLL is close to the average size of maturing individuals. 40 cm was a historic MLL for pike in Finland until 1993. An alternative procedure, HSL of 40-64.9 cm, was applied in the other two lakes

(Haarajärvi and Haukijärvi), representing the “modern“ length-based regulation, in which pike with intermediate size are harvested, and immature and large, reproductively valuable individuals are preserved. The lower threshold of HSL was the same as MLL, and the upper limit (≥65 cm) was selected to ensure a reasonable number (≥ 5% of the initial population) of individuals in the largest size class. In both procedures, half of the estimated biomass of the targeted sub-population was aimed to be removed each year.

Pike removal catch during 2008–2012 in HSL-lakes Haarajärvi and Haukijärvi consisted of 309 individuals and 150 kg (2.0–2.5 kg ha^{-1} yr^{-1}) and 32 individuals and 26 kg (1.9–3.6 kg ha^{-1} yr^{-1}), respectively. In MLL-lakes Hokajärvi and Majajärvi, the removal catch was 204 individuals and 123 kg (2.0–3.8 kg ha^{-1} yr^{-1}) and 108 individuals and 76 kg (3.5–5.9 kg ha^{-1} yr^{-1}) (**I**). Annual H_n (percentage of the removed numbers of individuals) was on average 31.6 and 54.7 % of estimated population number of pike ≥35 cm in HSL-lakes Haarajärvi and Haukijärvi, and comparably, 39.6 and 60.4 %, in MLL-lakes Hokajärvi and Majajärvi (**I**). The corresponding average removal percentages of estimated total biomasses (H_b) in the years 2008–2012 were higher in MLL-lakes Hokajärvi (50.1%) and Majajärvi (73.2%) than in HSL-lakes Haarajärvi (27%) and Haukijärvi (47.1 %).

3.4. Monitoring of fish food resources, habitat and water quality

Littoral vegetation (Estlander et al. 2009) macroinvertebrates, zooplankton and water quality (Estlander et al. 2010, Horppila et al. 2010, Olin et al. 2010) were monitored during the study, as part of other studies of the KESKALA project (Lehtonen et al. 2017). The water quality (nitrogen and phosphorus content, chlofofyll-α) and Secchi depth were monitored throughout the growing season (1-2 times per month), and furthermore once during autumn turnover and winter stagnation when also water color was measured. Oxygen concentration and temperature profiles were measured three times in July-August during standard gillnet sampling. In addition, temperature data were collected by temperature loggers from 1 m depth in May-October (**II**). Benthic invertebrates for stable isotope samples were collected in spring and summer 2009 from each study lake from three littoral sampling areas by kick net or by hand-picking. Zooplankton samples for stable isotope analysis were collected in July-August 2009 with 180 µm plankton net with vertical lifts (**III**).

3.5. Estimation of pike population parameters

From pike captured in mark-recapture, pike removal and fish assemblage monitoring (Nordic gillnetting), pike density, biomass, size- and age-structure, sex ratio and growth were determined. All caught pike were measured for length (total length, TL, 1 mm accuracy). Removed pike and released large (≥ 65 cm) individuals were weighed to the nearest 1 g and 10 g, respectively. Sex was determined, when possible, by running reproductive products, or from gonad preparation in cases when pike were killed. All individuals caught within a year were included in length distributions, in which either direct lengths (for pike caught in spring), or estimated spring lengths (for pike caught later) by back-calculated growth analyses, were used (**I**).

A modified Petersen method (Chapman version, Seber 1982) was used to calculate pike population size for autumn 2006 and spring 2007–2013 (**I**).

$$N_t = \frac{\{[(\sum_{t_0}^{t_{n-1}} T_{\geq 35\ cm}\ S)+1]\ (n+1)\}}{(m+1)-1} \qquad (1),$$

where t_0 and t_n are the first and the latest tagging year, $T_{\geq 35\ cm}$ is the total number of ≥ 35 cm tagged pike, *S* is the yearly survival rate, *n* is the sample size, and *m* is the number of marked individuals in a sample.

To evaluate S of marked pike in the above equation, total mortality for (Z) was estimated by the catch-curve method (Robson & Chapman 1961) from pooled age distributions in 2006–2008. Z was estimated to be 0.21, 0.32, 0.27 and 0.23 in Haukijärvi, Majajärvi, Hokajärvi and Haarajärvi, respectively. Z was assumed to be equal to natural mortality (M) since no fishing mortality affected the catch-curve estimates in 2006-2008 (**I**). Annual mortality (A) was then calculated as $A = 1 - e^{-Z}$, and $S = 1 - A$. It should be noted that in **IV**, S was based on smaller amount of age data (Kuparinen et al. 2012), resulting in different $T_{\geq 35cm}$ and, consequently, density estimates (**I, IV**).

Spring estimates were used when possible (not available in 2006) because they were more accurate due to higher number of individuals compared to the autumn estimates. 95% confidence limit intervals were calculated by Poisson or binomial distribution as suggested by Seber (1982). Estimates of pike biomass were based on population density estimates, length distributions and lake-specific length-mass power regression equations (**I**).

3.6. Estimation of age and growth

Age and back-calculated growth were determined by one experienced reader either from scales (released pike) of from cleithrum (removed pike) by using a Fraser-Lee equation (Frost and Kipling 1959) or a linear growth model (Casselman 1990). For yearly age distribution, either observed or estimated age (by age-length keys based on back-calculated length-at-age estimates, Horppila et al. 2010) was used (**I**). Growth parameters for 2013 (last year of the experiments) for production and consumption estimates (**II**) were not possible to determine by the methods described above, due to incomplete annuli. Therefore, growth in 2013 was estimated based on individual growth history, by using the von Bertalanffy growth equation, or, if not applicable, by the estimated average seasonal growth curve (Neumann et al. 1994) based on growth data from 2006-2012, or by the linear growth equation (Allen 1976).

3.7. Estimation of production and consumption by bioenergetic modelling

Pike production and consumption in the study lakes was modelled in article **II** by Fish Bioenergetics 3.0 (Hanson et al. 1997) based on the density estimates, average weight increment, natural and fishing mortality and observed water temperature assessed by the previously described methods. Lake and year-specific estimates were calculated for all ≥30 cm pike, and for pike size categories: small (30.0-39.9 cm), medium (40.0-64.9 cm) and large (≥65 cm). Default parameters of the program for pike (Hanson et al. 1997) were used in model, except for temperature, where the default optimum temperature for growth of all sized pike of the model (24°C) were replaced by more relevant values: For small and medium-sized pike 21°C and for large pike 19 °C (Pierce et al. 2013). Maximum temperature of 29.4 °C (Casselman 1978) was used for all pike. A 10 % weight loss by spawning (Lappalainen et al. 2013) was accounted for all pike ≥40 cm and 5 % for pike of <40 cm.

Prey items were divided into 3 subcategories with different energy content: fish (4186 Kj g^{-1}), invertebrates (3348 Kj g^{-1}) and non-fish vertebrates (amphibians and mammals, 4210 Kj g^{-1}). Relative frequencies of subcategories were derived from stomach content analysis for each lake separately, but the same proportions were used for all sizes of pike in all years (**II**). From bioenergetic analyses, three outputs were calculated: production of pike biomass (kg ha^{-1}), prey fish consumption by biomass (kg ha^{-1}), and production/consumption ratio, which indicates energy allocated for growth during the study period (Hanson et al. 1997, Christensen et al. 2009, Lin et al. 2012). Prey

species-specific consumption estimates were calculated only for the most important species, roach and perch (**II**).

3.8. Pike diet by stomach content analysis (SCA) and stable isotope analysis (SIA)

Dietary analysis was used in articles **II** and **III**. In **II**, such analysis was used to determine how consumption of pike is distributed between perch and roach. In **III**, the possible fishing-mediated change in diet for all size classes of pike was monitored. For dietary analysis, prey items were sorted taxonomically, counted and fish length was determined at 1 cm accuracy. Stomach fullness was assessed by the points method (Hynes 1950, Windell, 1971, Hyslop 1980), on a scale of 0-12 for each prey item separately (0 = empty stomach and 12 = absolute fullness, all prey items combined). To determine the importance of different prey items in pike diet, the indexes of absolute importance (*AI*) and relative importance (*RI*) were used (Hyslop 1980).

In SIA, the isotopic samples (fish, amphibians, invertebrates and zooplankton) were autoclaved or freeze dried, pulverized and 0.25-0.6 mg of the sample was analyzed for $\delta^{13}C$ and $\delta^{15}N$ by isotope ratio mass spectrometry. All isotope results are presented relative to international standards (Vienna PeeDee Belemnite for C and atmospheric nitrogen for N).

Trophic positions (TP) of pike, roach and perch were calculated by the equation of Post (2002);

$$(TP) = \lambda + (\delta^{15}N_{sc} - \delta^{15}N_{base}) / \Delta_n \qquad (2),$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ ($\lambda = 1$ for *Asellus aquaticus* was used), $\delta^{15}N_{sc}$ is the measured $\delta^{15}N$-value of secondary or higher consumer, and Δ_n is the enrichment in $\delta^{15}N$ per trophic level, in this case a value of 3.4 was used (Post 2002).

3.9. Evaluation of maternal effect

To evaluate fishing-mediated change in the reproduction effort of pike, egg and fry dry weights in relation to female size and age were compared in 2008 and 2012. From all females, randomly selected egg samples were dried and average dry weight was used as an indicator of egg quality, because it is tightly related to egg nutrient content and size of larvae (Ojanguren et al. 1996; Murry et al. 2008).

In 2008 experiments, starvation resistance of fry from different females was evaluated to determine whether female length affects the survival time of larvae with sole yolk sac reserves. From 16 females (TL=28.9–79.0 cm) a randomly chosen egg sample (9–20 g) was taken for fertilization experiments. Possible paternal effects were controlled by using milt from standard sized (TL=40.0–45.0 cm) male in fertilization. 13 females (length 28.9–79.0 cm) produced sufficient n of larvae (n ≥ 10 for one sample) to measure larval dry weight. From 12 of these larval sets, a subsample (n = 44–52) was taken to starvation experiments, where larvae were held in glass jars with sieved water (mesh size 25 µm), in the hatchery (average water temperature 10.9 °C, oxygen content within 7–10 mg l^{-1}). Dead larvae were counted and removed twice a day until the death of the last larvae.

3.10. Statistical methods

In article **I**, the year-to-year differences in frequencies of different sized pike, and female and male frequencies were analyzed by Fisher's exact test with pairwise comparison (Bonferroni correction). Tests were conducted for each lake separately by R Statistics ver. 3.1.0. The trends (2006–2013, except for Haarajärvi 2007-2013) in pike population density, biomass and mean length and age were investigated by general linear model (GLM) for each lake separately by SAS ver. 9.4.

In article **II**, the between-year differences in growth between 2008 and 2012 (first year vs. last year of pike removal) was analyzed by lake-specific repeated ANOVA with Wald statistics and Bonferroni corrections for pairwise comparisons. The yearly trends in 2008-2013 (the first year of the removal experiment and the last year of the study) in production, consumption and production/consumption ratio of different sized pike were examined by a GLM with repeated measures for each lake separately. A linear regression analysis was used to determine the effects of pike consumption on the estimated perch biomass in 2006-2013 (except in Haarajärvi 2007-2013). In the analysis, the yearly consumption estimates of pike were used to explain perch density estimates in the next spring or gillnet BPUEs of perch and roach in the coincident year.

In article **III**, possible between-year and between-lake differences in the stomach contents were analyzed with MANOVA, including the independent variables lake, year and pike length class, as well as all their interactions.

The effects of lake, year, length and growth (measured as length increment (LI) in the previous year) on trophic position was analyzed by a GLM. Also the effects of lake, year, length and growth (measured as length increment (LI) in the previous year) on TP was analyzed by a GLM.

To assess the effects of stomach contents on the TP of pike, the pike with both stomach and SIA data were divided into four stomach categories: empty stomach (n=100), macroinvertebrates in stomach (n=13), only fish in stomach (n=129), and amphibians in stomach (n=5, no mammal occurred in stomachs of these pike). The effect of stomach category, lake and year (and all their interactions) was analyzed with ANOVA.

In article **IV**, the effects of female length and age on the dry weight of eggs and larvae were analyzed with linear mixed models including length and age (linear, quadratic and cubic effects) as continuous variables, year as a categorical variable and lake as a random variable. The effect of female length on survival time of larvae with bare yolk sac reserves was analyzed by Cox regression (SPSS 15.0). Temperature sum (accumulated degree days above a threshold temperature of 0 °C, Kotlyarevskaya, 1969) was used as the time variable, death of each larvae as status variable and female length as continuous covariate, and temperature sum x female length as a time-dependent covariate (Cox 1972). For all above analysis, the normality of data was checked, and logarithmic or arcsin –transformation was used if needed.

4. MAIN RESULTS

4.1. Responses in population density and biomass (I)

Pike pre-treatment density estimates (average of 2006–2008, except in Haarajärvi 2007–2008) were 14.8 and 9.2 indiv. ha^{-1} in HSL-lakes Haarajärvi and Haukijärvi, and 11.4 and 16.5 indiv. ha^{-1} in MLL-lakes Hokajärvi and Majajärvi. Corresponding biomass estimates were 9.3, 11.3, 8.1 and 13.3 kg ha^{-1} in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Fig.2). Large ≥ 65 cm pike comprised on average 12.8 and 46.8% of the estimated total density and biomass in Haarajärvi, 21.9 and 46.6% in Haukijärvi, 7.2% and 19.4% in Hokajärvi and 5.5% and 19.8% in Majajärvi (Fig. 2).

Pike population density decreased in both MLL-lakes. In Majajärvi, both density (GLM, t= –4.60, df=6, p=0.004) and biomass estimates (GLM, t= –4.21, df=6, p=0.006) decreased. In Hokajärvi, biomass estimate

decreased significantly (GLM, t= –3.87 , df=6, *p*=0.008), but density did not. In HSL-lakes, statistically significant trends in abundance estimates were not detected, although density decreased 26.7 and 25.1 % and biomass 30.1 and 38.8 % in Haarajärvi, and Haukijärvi, respectively.

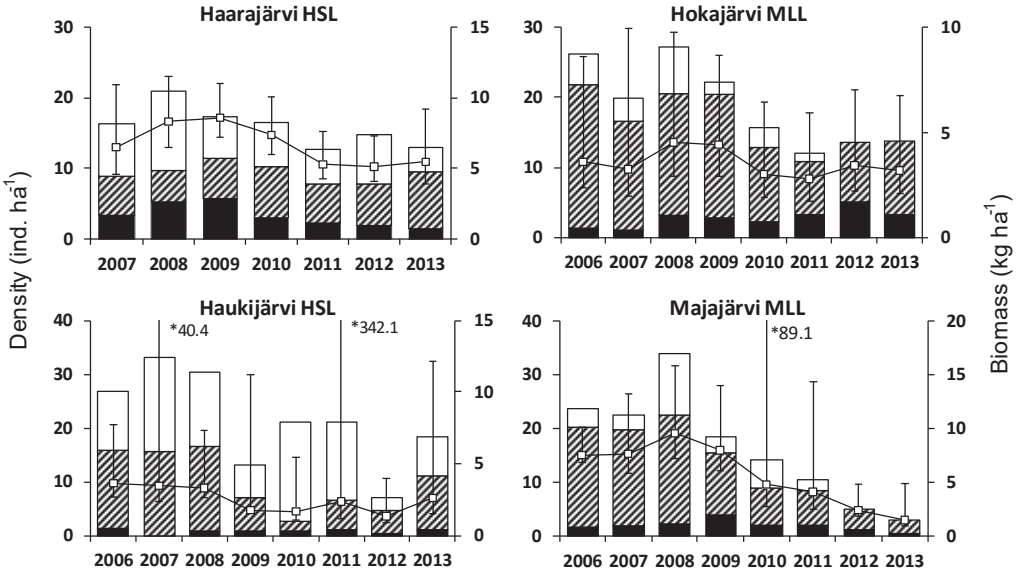

Figure 2. Pike density estimates with 95% confidence limits (line) and biomass estimates with proportions of 35-39.9 cm (black column), 40-64.9cm (pattern column) and ≥65 cm pike (white column) in research lakes in years 2006-2013. MLL = Minimum length limit, HSL = Harvestable slot-length limit. Removal fishing of pike ≥40 (MLL) or 40-64.9 cm (HSL) was conducted in 2008-2012. Modified from ***I****.*

4.2 Responses in pike population structure (I)

Pike populations structure showed a clear response to MLL in Majajärvi and Hokajärvi. In Majajärvi, pre-treatment mean size (2006-2008 average) of pike was 45.3cm, a value which decreased 6.8% during study (GLM, *t*= –4.33, df=6, *p*=0.005). Length distributions in years 2012 and 2013 were severely truncated, compared to years before pike removal (Fig. 3). However, no differences between the annual frequencies of different sized pike were observed (Fisher's exact test: *p*>0.05), as truncation occurred within the medium size-class. In Hokajärvi, pike mean size was initially 46.7 cm and it decreased 9.5% (GLM, *t*=–4.34, df=6, *p*=0.005) during study and size-structure-distribution shifted towards a dominance of <45 cm pike towards the end of the study (Fig. 3). Truncation of size distribution was also expressed

by development of frequencies of different-sized onto increase of small pike between pre-removal and late removal years in Hokajärvi (Fisher's exact test, $p<0.05$). In both MLL-lakes, large pike were completely extinct after four years of pike removal (Figs. 2 and 3).

HSL maintained the demographic structure of the pike population. Pike average pre-removal lengths (2006–2008 average) were 42.7 and 53.0 cm in Haarajärvi and Haukijärvi, and no statistically significant decreasing trends in mean size were detected (**I**). In addition, large pike remained in populations until the end of the study, indicating the advantageous functioning of the HSL and the tolerance of pike to C&R-fishing (Figs. 2 and 3). In Haarajärvi, the density of harvestable-sized (40-64.9 cm) individuals was the greatest in the last year of experiment, indicating increased recruitment and growth. Pike size structure in Haukijärvi did not change statistically significantly, but the length distribution fluctuated during the study period, due to small sample size.

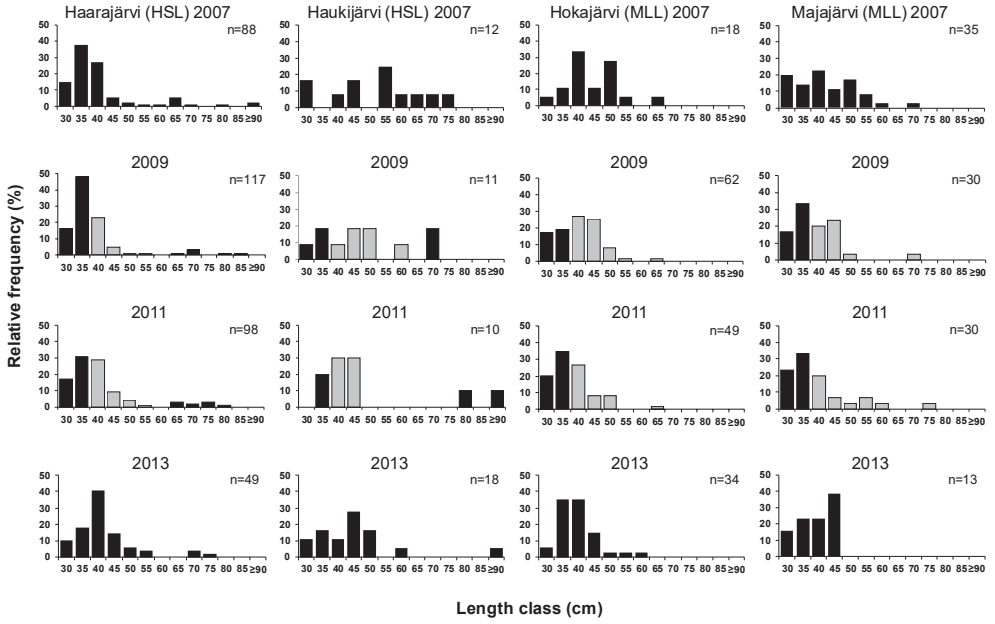

Figure 3. Pike length frequency distributions in study lakes in spring of years 2007, 2009, 2011 and 2013. Grey colour refers to removal fishing years and subjected size-classes. HSL = Harvestable slot length limit, MLL = Minimum length limit. Modified from ***I***

Pike average age had a statistically significant decreasing trend in both MLL-lakes Hokajärvi (Fisher's exact test, $p=0.017$) and Majajärvi (Fisher's exact test, $p=0.002$). Average age before pike removal (2006–

2008 average) was 7.4 yr. in Hokajärvi and 6.7 yr. in Majajärvi, from which it decreased to 6.4 yr. in Hokajärvi (GLM, t=–3.28, df=6, p=0.017) and to 5.5 yr. in Majajärvi (GLM, t=–5.42, df=6, p=0.002) until 2013. In HSL-lakes Haarajärvi and Haukijärvi no negative trend was detected, as in Haarajärvi mean age remained quite consistently between 5.9–7.7 yrs. (lowest in 2013). In Haukijärvi mean age had high variation between 5.9 and 10.7 yrs. (**I**). The share of younger age classes (especially <3 yr.) increased during the study period indicating increased recruitment. In all study lakes, old (≥12 yr.) pike remained in the population until the end of the study (**I**).

Average female percentages during the study were 41.2%, 54.6%, 49.2%, and 41.6%, in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively. The proportion of females in the removal catch was larger compared to total number of pike caught. However, the female/male ratio did not shift towards male dominance even in MLL lakes, where large individuals, which are often females, were targeted (Fisher's exact test, p>0.05).

4.3. Pike growth (II)

Pike growth was low in study lakes, as six-year old pike were on average 39.2, 40.5, 37.0 and 39.1 cm (TL) in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Fig. 4).

Pike growth increased in all study lakes other than Majajärvi as a response to removal fishing, which was indicated by an increase in length-at age from 2008 to 2012 (**II**). In Haarajärvi, the response was the clearest of all study lakes, and length-at-age increased in all age groups from 2-10 yr. (repeated ANOVA, p<0.05). In Haukijärvi the growth response was less clear, as the increase in length-at-age was statistically significant (repeated ANOVA, z=-3.8, S.E.=0.070, p<0.001 for 3 yrs. and z=-7.6, S.E.=0.044, p<0.001 for 6 yrs.) only in age groups 3 and 6 yr. (**II**). Of MLL-lakes, pike growth was positively affected in Hokajärvi, as pike length-at-ages of 2, 4, 5 and 10 yrs. old pike increased (repeated ANOVA, p<0.05). In the other MLL-lake Majajärvi, pike growth did not show a positive response, but the only statistically significant response was the decrease in length-at-age of 12-year-old pike (repeated ANOVA, z=3.19, S.E.=0.106, p=0.010).

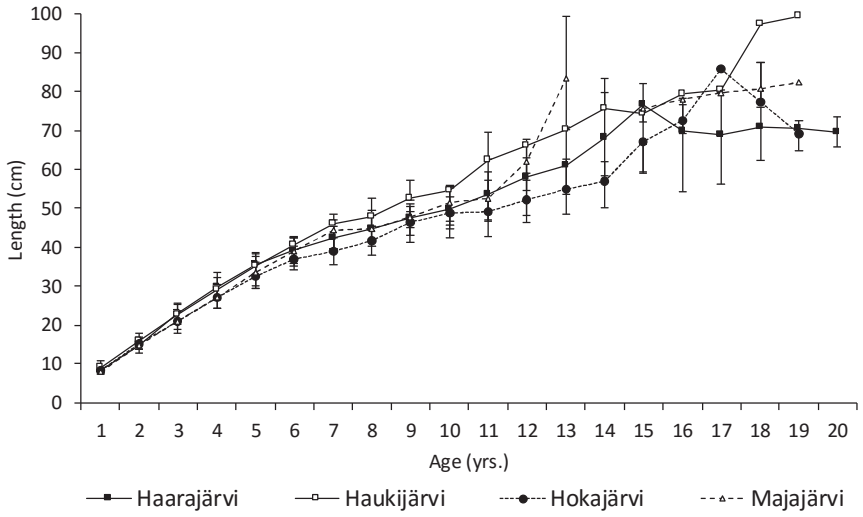

Figure 4. Average length-at-age curves with SDs of pike in the study lakes in 2006-2012.

4.4. Pike production (II)

The production of ≥30 cm pike population in 2006-2013 (2007-2013 in Haarajärvi) was on average 2.4 (SD 0.72) and 2.1 (SD 0.88) kg ha^{-1} yr^{-1} in HSL-lakes Haarajärvi and Haukijärvi, and 1.9 kg ha^{-1} (SD 0.51) and 2.3 kg ha^{-1} (SD 1.36) in MLL-lakes Hokajärvi and Majajärvi (Fig.5). The production of large pike consisted on average 17.5 and 38.4 % of the total production in HSL-lakes Haarajärvi and Haukijärvi, and 8.5 and 10.2 % in MLL-lakes Hokajärvi and Majajärvi.

In both HSL-lakes, pike production first decreased but later recovered to (or above) the initial level by the end of the study period. No statistically significant (GLM: $p>0.05$) trend in production of pike of any size-class was perceived from 2008 to 2013.

In MLL-lakes, pike production expressed different responses to pike removal. In Hokajärvi, production first decreased and then recovered, because of increase in production of small pike (GLM: $t=3.43$, df=4, $p=0.027$). In the other MLL-lake, Majajärvi, pike production decreased from a level of 3.7 kg ha^{-1} (2006-2008 average) to <1 kg ha^{-1} in 2013, and the decreasing trend was significant (GLM: $p<0.05$) for all size-classes (**II**).

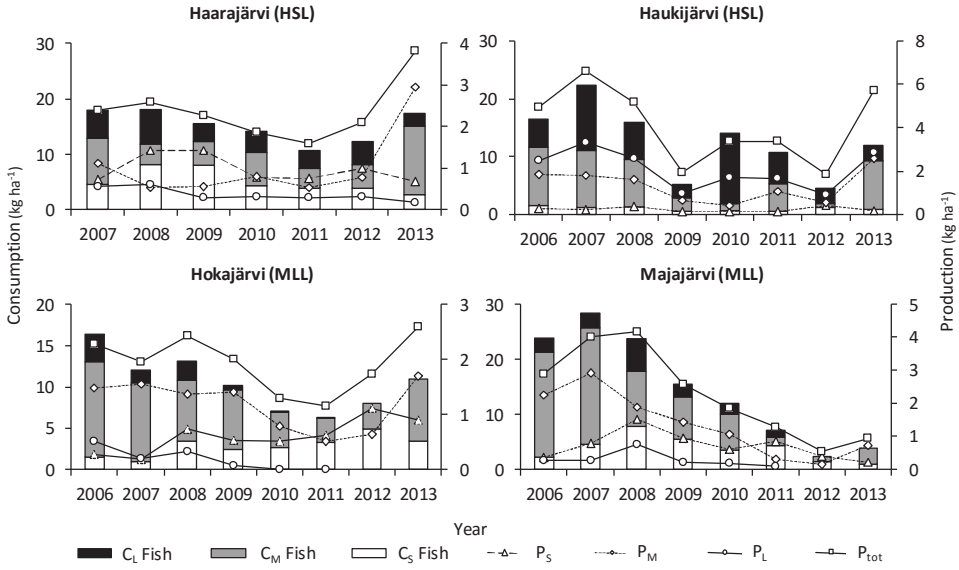

Figure 5. Development of pike production and consumption of fish by total population (P_{tot} and C_{tot} = total height of the bar,), 30.0-39.9 cm (P_S and C_S), 40.0-64.9 cm (P_M and C_M) and ≥65 cm (P_L and C_L) in 2006-2013, except in Haarajärvi in 2007-2013. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation. Note different scales of both y-axis.

4.5. Pike consumption (II)

The total consumption of pike on prey fish was on average 18.4 (SD 9.3) and 12.6 (SD 5.9) kg ha^{-1} in HSL-lakes Haarajärvi and Haukijärvi and 10.5 (SD 3.41) and 14.6 (SD 9.9) kg ha^{-1} in MLL-lakes Hokajärvi and Majajärvi (Fig.5). The consumption by large pike represented on average 27.3, 47.6, 9.8 and 15.8 % of the total consumption in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively.

In MLL-lake Majajärvi, the total consumption by the pike population during the study period was initially the highest of the study lakes, 25.3 kg ha^{-1} (2006-2008 average), but it decreased to <4 kg ha^{-1} until 2013 (GLM: t=-5.85, df=4, p=0.002). In Hokajärvi, the total consumption did not have any significant trend (GLM: $p > 0.05$). In HSL-lakes no clear trend was detected (GLM: p>0.05). The total consumption first decreased from 18.1 (2008) to 10.8 kg ha^{-1} (2011) in Haarajärvi and from 15.9 (2008) to 4.6 kg ha^{-1} (2012) in Haukijärvi, but the consumption recovered in both lakes by 2013.

4.6. Pike trophic position by diet and SIA, and the effects on prey fish populations (II, III)

Altogether 15 different prey items were identified from pike stomach contents including six fish species. Of 542 stomachs studied, 51.1% were empty, and of those with content, 97% included fish, 10% macroinvertebrates, 3% amphibians and 2% mammals. Roach and perch were clearly the most important food items, contributing 84% of the total stomach volume. The probability of invertivory decreased with pike size but not quite significantly (Logistic regression: Wald $X^2_{1,1}$=3.064, p=0.080)(Fig. 6). The probability to eat amphibians or mammals increased strongly in large pike (Logistic regression: Wald $X^2_{1,1}$=13.047, p<0.001). Prey length increased with pike size (linear regression: r^2=0.105, $F_{1,292}$=34.19, p<0.001).

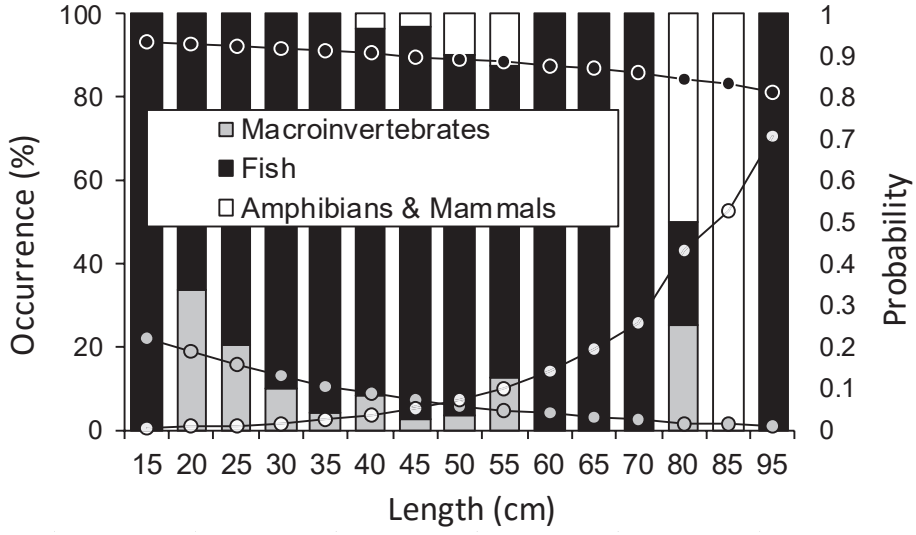

Fig 6. The observed occurrence of macroinvertebrates (grey bar), fish (black bar) and amphibians and mammal (white bar) in pike stomach containing food, and modelled probability by logistic regression of fish (black dotted line), macroinvertebrates (white dotted line) and amphibians and mammals (grey dotted line) in pike stomach.

Pike population consumed on average 31.8 - 60.4 % of the estimated perch spring biomass in the study lakes in 2006-2013 (**II**). A statistically significant negative relationship between pike consumption on perch and perch gillnet BPUE was observed in Majajärvi (linear regression, p = 0.038), but not no other statistically significant relationships between pike consumption and indicators of prey fish abundance were found.

Pike had the highest $\delta^{15}N$ and TP values of all trophic categories and was at the top of the food web in all of the lakes in most of the years (Fig. 7). In the year 2013 Majajärvi and Haukijärvi, pike $\delta^{15}N$ values were close to those of roach and perch. In all three species, $\delta^{15}N$ values decreased from 2008-2009 to 2013 (Tukey: p<0.001-0.007). The $\delta^{13}C$ values in pike, as well as in roach and perch, were closer to invertebrate than zooplankton values, indicating that a major part of the carbon in pike originates from littoral sources.

TP increased with pike length (GLM: F=165.89, *df*=1, p<0.001). On average, 20, 40, 60 and 80 cm pike had TP of 3.60, 4.00, 4.24 and 4.40, respectively. TP of 40 cm pike decreased from 4.05 in 2008-2009 to 3.93 in 2013. Length increment had a small negative effect on TP, and on average in 40 cm pike, TP decreased 1.47% when LI increased from 2.9 cm to 11.7 cm (i.e. from half to double of the average LI).

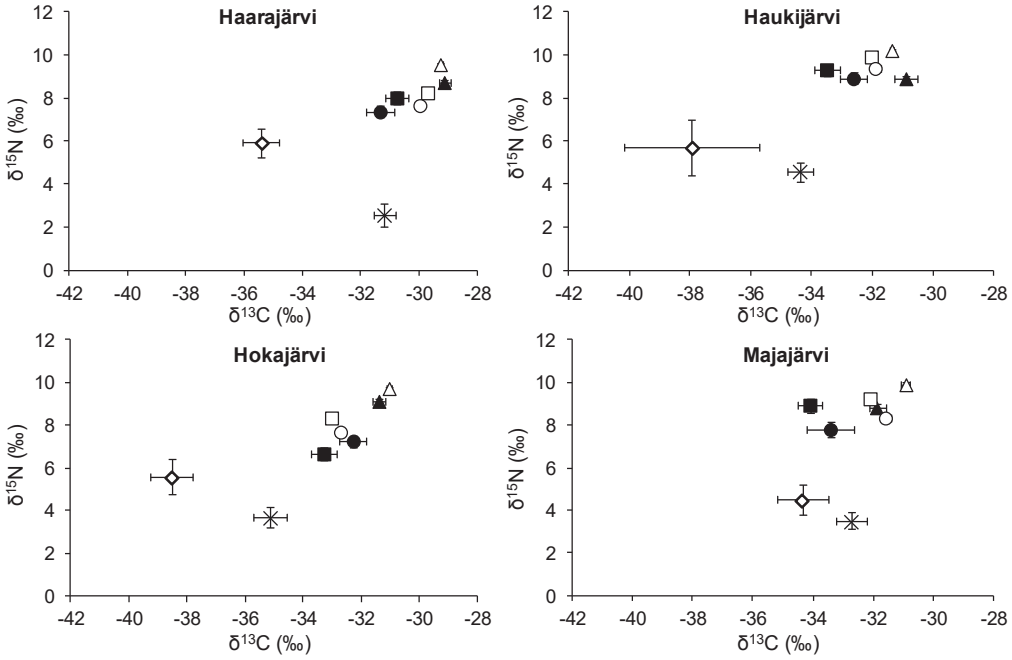

Fig. 7. Stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of different trophic categories in the study lakes: asterisk = macroinvertebrates, diamond = zooplankton, circle = roach, square = perch, triangle = pike. White symbols (and asterisk) represent values in 2008-2009, black symbols in 2013. In fish, SIA-values represent average size individuals: 14 cm perch and roach, and 42 cm pike. Error bars denote standard error (SE).

The stomach category “macroinvertebrates in stomach” had the lowest average TP (3.86) and it differed significantly from the TP in the stomach category “only fish in stomach”, TP=4.08 and almost significantly from the category “empty stomach”, TP=4.02 (Tukey= 0.009 and 0.055, respectively.

The $\delta^{13}C$ and $\delta^{15}N$ values in both the uncleaned and purified fin-SIA samples correlated significantly with the corresponding values in the muscle-SIA samples. However, the $\delta^{13}C$ values of the fin-SIA were significantly higher than the values of muscle-SIA (ANOVA: $F_{2,177}=10.99$, $p<0.001$), for both cleaned (Tukey: $p=0.003$) and uncleaned fin samples ($p<0.001$). The cleaning reduced the average muscle-fin-difference in $\delta^{13}C$ values from 4.2% to 2.8%. The $\delta^{15}N$ values in muscle and cleaned or uncleaned fin samples did not differ statistically (ANOVA: $p>0.100$). However, the interception in the regression between $\delta^{15}N$ values in muscle and fin samples differed from zero (p= 0.038 and 0.076 for uncleaned and cleaned fin samples, respectively) indicating larger differences in higher $\delta^{15}N$ values.

4.7 Maternal effect (IV)

Female length and age had a positive effect on egg dry weight (linear mixed model, $p=0.023$ and p=0.046). The eggs in year 2012 were heavier than in 2008 (linear mixed model, $p=0.023$) in relation to female length (Fig. 8). The effect of length was different on egg dry weight depending on the age (linear mixed model, $p=0.044$), and for young pike (<6 yrs.) the effect was always positive, but for older pike effect was lower or even negative. Year * length –interaction was significant (linear mixed model, $p=0.001$), as in 2012 the effect of length was positive for females at all ages, and the largest and youngest females produced the heaviest eggs according to model. The dry weight of larvae had a significant positive correlation with female length (linear mixed model, $p=0.016$).

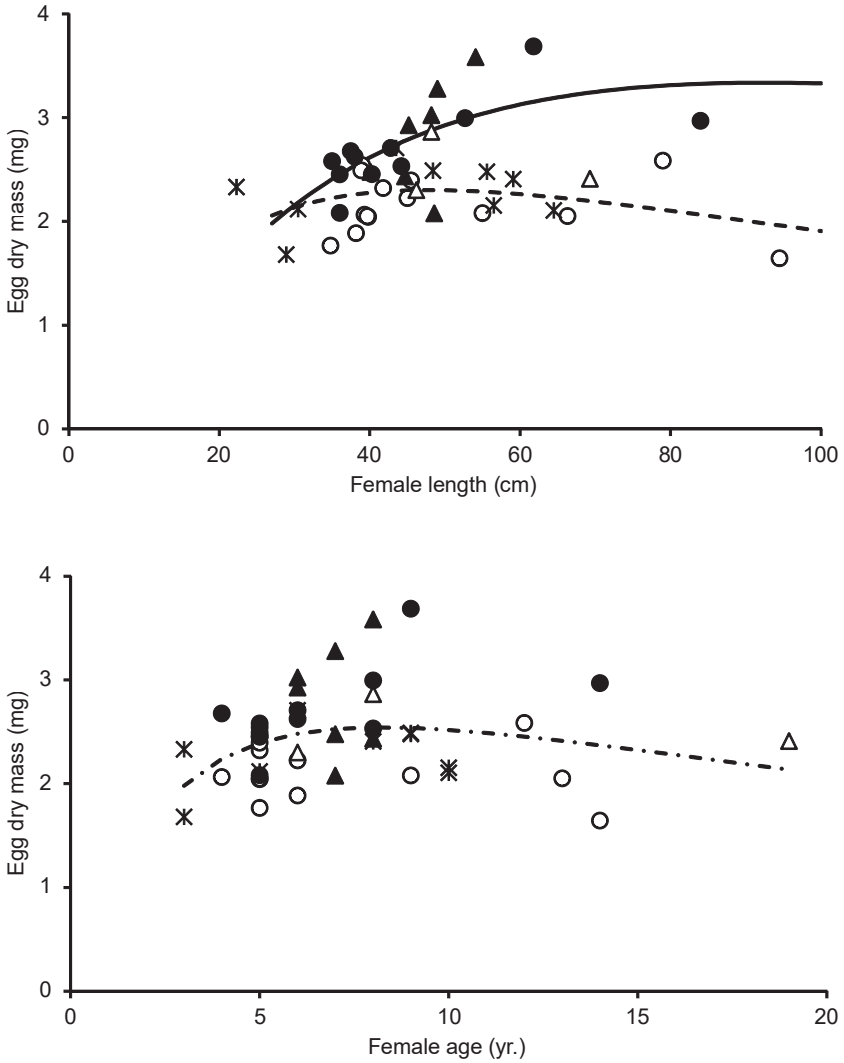

Fig 8. Effect of pike female length (above) and age (below) on larval dry weight. Symbols refer to data of different lakes in 2008: circle = Haarajärvi, triangle = Hokajärvi and asterisk= Majajärvi.

Starvation resistance of the first hatched larvae with bare yolk sac reserves was on average 450 °days (°C, range 406 to 492 °days)(Fig. 9). Starvation resistance had a significant positive correlation with female length (Cox regression, p=0.009). The model estimated that the larvae from the largest females survived longer and survival rates remained over 0.7 before a steep decrease after degree day 433 (Fig. 9). The larvae from the smallest female were estimated to die sooner and had survival rates lower than 0.7 already at a degree day 341.

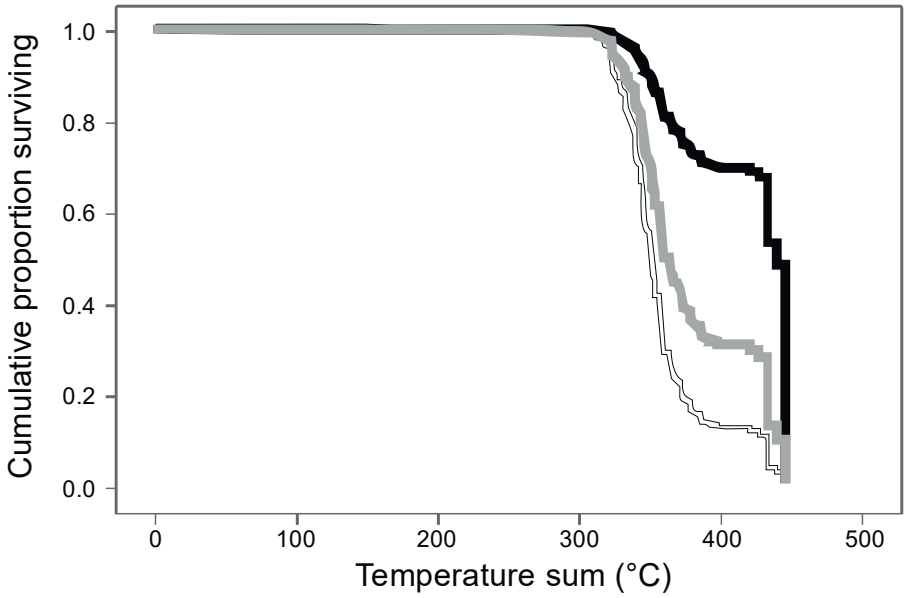

Fig. 9. Cumulative survival of pike larvae with yolk sac reserves according to Cox regression model. White, grey and black lines represent modelled survival curves of larvae from 29-, 46- and 79-cm females, respectively. The sizes of the females represent the minimum, median and maximum size of females that produced larvae for survival experiments.

5. DISCUSSION

5.1. Responses in pike population density and demographic structure

Study **I** indicated the sustainability of HSL compared to MLL. HSL retained large pike in the population, which is considered an essential feature in sustainable fishing (Arlinghaus et al. 2010, Gwinn et al. 2015). It also maintained pike population density, biomass and size structure close to original levels in spite of the fishing pressure. Increased recruitment was observed in Haarajärvi, indicating that HSL would not have decreased population abundance considerably even if the fishing had continued. This was emphasized by the highest observed frequency of harvestable sized pike in 2013, the last year of the study. In the smallest lake Haukijärvi, fluctuating abundance and structure estimates, possibly due to limited sample size, prevented reliable detection of possible trends. However, small populations are also prone to high between-year variation due to environmental and demographic stochasticity (Lande 1993).

Study **I** support earlier studies (Pierce et al. 1995, Arlinghaus et al. 2010, Pierce 2010) that criticize MLL with low threshold limit to be unable to maintain viable pike populations. Different responses in population density in Hokajärvi and Majajärvi are likely explained by considerably larger removal percentage in Majajärvi in 2011 and 2012, which led to a collapse of the pike population. Lake morphology may also affect the vulnerability of pike population to fishing. In Majajärvi small size, steep banks and narrow euphotic depth restrict macrophytes (and habitats for pike) along the shoreline, which have likely increased pike catchability especially in angling. The large vegetated littoral areas in Hokajärvi may have decreased catchability as pike are distributed over a wider area, as observed in walleye (*Sander vitreus*) (Hansen et al. 2005), but also contributed to effective reproduction and compensatory recruitment for small pike (Bry 1996).

Study **I** also indicated that the age structure of the pike population may be less affected by fishing compared to the size structure. The effect on age distribution was not as evident compared to alterations in size-structure, as old (≥12 years) pike remained to some extent in both MLL-lakes until end of the study. This finding implies that large individuals were more vulnerable to fishing as Pierce and Tomcko (2003) have suggested, indicating that MLL favours slow-growing and passive individuals at the expense of fast-growing and actively feeding individuals.

MLL should decrease the number of female pike more than that of male, as large pike, that are more likely females, have higher probability of being caught (Craig 1996, Lewin et al. 2006). Loss of females has detrimental effects on recruitment (Lewin et al. 2006). This was partially supported by study **I**, as more females than males were included in the removal catch. However, the ratio of females and male did not shift towards male dominance even in MLL lakes, where large individuals were targeted.

5.2. Fishing-induced growth response

The growth responses in exploited pike populations may be highly dependent on the abiotic and biotic circumstances in the lakes (Diana 1983, Margenau et al. 1998, Rask et al. 1999). Pike growth increased in study lakes other than Majajärvi as a response to removal fishing (**II**). The response was clearest in Haarajärvi, the only study lake with a well-oxygenated hypolimnion (Olin et al. 2010), which may have contributed to the increased growth (Margenau et al. 1998). A deep oxygenated layer is especially crucial for growth of large pike, as they have higher

oxygen demand than smaller individuals (Diana 1996, Pierce et al. 2013).

Of MLL-lakes, pike growth was positively affected in Hokajärvi, with the highest littoral vegetation coverage (80 %) and water transparency, both of which may have contributed to the strong growth response of small pike (Bry 1996, Casselman 1996). Hokajärvi is also the most oligotrophic of the study lakes, and has the lowest perch population density (Olin et al. 2016), indicating that pike growth may have been limited by food competition, and removal fishing released these resources for remaining individuals.

In the other MLL-lake Majajärvi, no positive response in growth was observed, but the growth of old pike decreased. This may indicate the disappearance of large and fast-growing individuals (**I**, **II**). Despite the initially highest pike density and productivity (Olin et al. 2016), no positive response in growth or recruitment occurred in Majajärvi. The result underlines the vulnerability of pike to MLL-type fishing especially in challenging environmental conditions. If fast-growing phenotypes are removed by fishing, and the remaining slow-growing and early-maturing individuals may be unable to utilize the released resources for growth. (Diana 1983, Kokkonen et al. 2015).

Pike growth in this study was slow, but comparable to that in the study of of Raitaniemi (1995), in which pike reached a length of 35 on average cm at age 4 yrs. Slow growth of pike is a well-documented phenomenon in humic lakes (Craig 1996, Rask et al. 1999). In their study in 19 small northern Wisconsin lakes, Margenau et al. (1998) observed stunted growth of pike after TL of 53 cm due to variety of environmental and density-related factors, such as high temperature, low oxygen content, high pike density and prey type, size and availability. Unfavorable conditions likely explain the slow growth in this study as well, as the lakes are oligo-mesotrophic and have strong temperature stratification and consequently hypoxic hypolimnion (except Haarajärvi) during summer and winter, restricting fish to a thin oxygenated layer (Rask et al. 1999). Study lakes have also low euphotic depth and steep banks, and littoral vegetation is narrow (coverage 4-15 %, except 80% in Hokajärvi), resulting in limited habitats for pike and its prey species (**I, II**). Casselman & Lewis (1996) and Margenau et al. (1998) concluded that extensive littoral vegetation is beneficial for growth of small pike, but not for larger individuals. Margenau et al. (1998) observed increased pike growth in low visibility conditions, but it was likely due to lower productivity of clear lakes. Hokajärvi is the most oligotrophic of the study

lakes, but has the highest vegetation coverage and water transparency. Hokajärvi seemed to produce small pike despite pike removal (**I,II**), but large pike were sparse even before the start of pike removal (**I**).

For large pike the only growth response was the decreased growth of 12 yrs. old pike in Majajärvi. Growth of large pike was not positively affected by removal fishing, because their foraging capabilities are likely not constrained by intraspecific or intraguild competition or risk of cannibalism due to their large size and low number (Raat 1988, Grimm & Klinge 1996). However, catch and release fishing (including tagging) has been reported to cause decreased growth of pike (Klefoth et al. 2008) and large pikeperch (Stålhammar 2013), which may partially explain why growth response was not perceived in large pike.

5.3 Responses in production and consumption

The responses in production and consumption of pike reflected the changes in abundance, growth and demographic structure of pike, and environmental characteristics of study lakes. The observed average production (1.9-2.4 kg ha^{-1} yr^{-1}) is comparable to an earlier study (Rask & Arvola 1985) in the same area (2.6 kg ha^{-1} yr^{-1}), but roughly half of the average of 4.07 kg ha^{-1} yr^{-1} estimated by Pierce & Tomcko (2003) in seven lakes in Minnesota. Production by large pike contributed to a higher proportion of total production in HSL-lakes, as the initial proportion of large pike was greater (**I**), and gradual disappearance of large pike from MLL-lakes further decreased their consumption. The latter indicates another negative impact of harvesting large individuals, because their low turnover ratio increase vulnerability to overfishing (Pierce & Tomcko 2003, Arlinghaus et al. 2010).

The results indicate the potential of pike populations to compensate fishing mortality under HSL and resilience to fishing, since in the HSL-lakes, pike production first decreased but later recovered to or above the initial level. According to our study, HSL can maintain pike production provided that the growth rate is enhanced. The applied HSL on 40-64.9 was suitable for the study lakes with low production and slow pike growth (**I**, **II**). Consequently, in more productive waterbodies, higher HSL would be advisable. In Sweden, in the coastal waters of the Baltic Sea, a 40–75 cm HSL is set for pike with daily bag limit of three pike, in response to the declining pike stock in this region, and the study of Arlinghaus et al. (2010) suggested that the optimal HSL for maintaining large pike is achieved by setting the lower length to threshold 40 cm and upper threshold to 75–80 cm.

Under MLL the pike production response to fishing varied. In Hokajärvi, the observed recovery of production can be explained by increase in density (**I**) and increase in growth of small and young pike, which compensated the fishing mortality (**II**). In the other MLL-lake, Majajärvi, pike production decreased considerably, because no compensative responses (increased growth or recruitment) occurred (**II**). This supports the recent criticism of MLL by Arlinghaus et al. (2010), Pierce (2010) and Gwinn et al. (2015), according to whom low MLL and high exploitation rate may lead to decrease in yield.

The low overall production of study lakes might increase the vulnerability to fishing. According to Pierce & Tomcko (2003), recreational fisheries in Minnesota can annually harvest all of the production of pike, which has led to high densities of small individuals. With low production rates, overfishing is likely to occur even under moderate fishing pressure (Mosindy et al. 1987). In northern American recreational fisheries, an extensive effort has been made to improve productivity and size-structure (for trophy pike) of stunted populations, by releasing resources through harvesting small pike, but with limited success (Pierce & Tomcko 2003, Pierce 2010).

Consumption analyses indicated that HSL preserved the role and influence of pike in the ecosystem (**II**). Pike consumption in HSL-lakes followed the same response-pattern observed in production: an initial decrease followed by a recovery. All size classes contributed to the total consumption, suggesting that pike population has the potential to consume diverse-sized prey, thus widely affecting the food web structure (Nilsson et al. 2001).

In MLL-lake Hokajärvi, total consumption remained close to the level before pike removal, as the consumption of small-sized pike increased and compensated the lost consumption of large pike (**I**). In Majajärvi, where pike population density and biomass decreased, pike consumption by all size-classes declined, suggesting the detrimental effects of heavy exploitation under MLL on the ecosystem effects of pike.

5.4. Effects of pike size and fishing on diet and trophic position

The observed diverse diet in the study lakes supported earlier studies (Frost 1954, Diana 1979) of the opportunistic nature of pike. The high share of roach and perch in the stomach contents reflected the dominance of these species in study lakes (Olin et al. 2010). More than half of stomachs were empty, which is typical for piscivorous fish, due to

their rapid gastric evacuation rate, and tendency to ingest single prey at once (Anderson 1999).

The presence of abundant and appropriate sized prey is crucial for pike growth (Margenau 1998). The importance of non-fish prey (macroinvertebrates for smaller and amphibians and mammals for larger pike), and relatively small prey size of large pike indicates the resource limitation for pike (**I-IV**), which is a common phenomenon in humic lakes (Tonn & Magnuson 1982, Rahel 1984, Rask 1999). It also reveals the importance of littoral zone as a source of energy for pike (Vander Zanden and Vadeboncoeur 2002).

Pike had the highest trophic position (the highest TP and $\delta^{15}N$ -values) of all studied species, indicating its top predator status. The increase of TP with pike length is likely a result of diet containing prey from upper trophic levels, such as predatory perch and other pike, although the largest prey fish were observed from stomachs of intermediate sized pike. A possible reason for the observed exceptionally low $\delta^{15}N$ values in Majajärvi in 2013 is that intensive removal fishing left only passive (and possibly invertivorous) individuals remaining in the lake. This is supported by the lack of growth response to fishing in the lake.

Trophic position of pike decreased from 2008-2009 to 2013 in all study lakes even though pike diet remained similar and no reduction in the share of fish in stomach contents was observed. This may be due to increased growth by pike removal (except in Majajärvi). Gannes et al. (1998) and Gaye-Siessegger et al. (2007) showed a connection between increasing $\delta^{15}N$ values and slow growth and decreased condition factor. Length increment had negative effect on trophic position. The negative effect of growth on TP and $\delta^{15}N$ can decrease their reliability as index of trophic status in pike, because fish prey with high nutritive values promotes the growth of pike, and pike consuming fish should have high TP.

In **III**, the connection between SCA and SIA was established: the invertivorous pike had lower TP than exclusive fish eaters, or individuals with empty stomach (Beaudoin et al. 1999). The variation in the TP results reflect to the diverse feeding behavior of pike (Paradis et al. 2008; Beaudoin et al. 1999, Pedreschi et al. 2015). In general, SCA provides direct and specific information of taxa ingested shortly before capture and SIA a long-term diet (Beaudoin et al. 1999, Syväranta 2008). The increase of TP by SIA and the decrease of invertivory by SCA in relation to pike length further support that the SCA also can give information of the long-term diet. In addition, the individuals with empty

stomach had relatively high TP, indicating that pike with empty stomach are likely piscivorous (Chapman et al. 1989, Paradis et al. 2008). Large share of empty stomach is typical for piscivorous fish, due to their rapid gastric evacuation rate (Anderson 1999).

The fin-SIA samples correlated significantly with the muscle-SIA samples, which support earlier studies in other species (Jardine et al. 2011, Kelly et al. 2006, Sanderson et al. 2009). Therefore, pike need not be killed to get reliable results for SIA. This is an important asset when collecting samples from large pike, which are important for pike population persistence (Arlinghaus et al. 2010, Matsumura et al. 2011, **I**, **II**, **IV**), ecosystem functioning (Kuparinen et al. 2016, **II-IV**), and for recreational fishing (Paukert et al. 2001, Arlinghaus et al. 2007, Carlson 2016). Therefore, cleaning of fin samples and using of the correction equations is recommended to improve the comparability further.

5.5. Maternal effect

The quality of progeny (indicated by heavier eggs and larvae) increased in relation to female size, but the result was not straightforward, as the very oldest and largest females had relatively low egg weight in 2008 (**IV**). The environmental conditions described earlier, and the slow growth of large pike in the study lakes (**II**) might explain this result. It is possible that largest individuals are not able to get enough energy to retain the quality of their reproductive products (Kamler 2005, Edeline et al. 2007). In their study in Windermere, Edeline et al. (2007) found, that pike displayed a tradeoff between growth and reproduction: gonad weight was lower in females with fast growth compared to slow growth. Although in **IV** egg weight was not negatively related to female growth, a tradeoff between growth and reproduction is supported by the observation that pike females produced heavier eggs in relation to their size in 2012 compared to 2008, because heavy exploitation of pike stocks enabled a higher investment in reproduction.

It is important to notice, that in **IV** we were able to observe decreased egg dry weight in the oldest female, since the study lakes are prohibited from fishing, and very old (maximum observed age 22 yr.) individuals are included in the populations. In other studies, degradation of egg quality may not have been detected because old individuals are missing due to high fishing mortality (Kamler 2005). In addition, the dependence of the maternal effect on female age may partly explain why the correlation between maternal size and offspring quality has not been found in some studies (Wright & Shoesmith, 1988, Murry et al. 2008). The highest dry weight of eggs and larvae was observed at a relatively

high female age (9 years), which suggests that best quality of eggs is probably achieved after several spawnings. Since the quality of reproductive products does not decrease until females become very old, and as the amount of eggs is multifold in large females (Craig 1996, Venturelli 2010), large females are important for the reproduction of pike populations. This should be taken into account in fisheries management, e.g. when imposing size limits on fishing, as also stated in the simulation study of Arlinghaus et al. (2010) and Matsumura et al. 2011, and suggested by Venturelli et al. 2010.

Study **IV** also showed that larvae from larger females had better starvation resistance, which improves the persistence of pike larvae solely on yolk sack reserves. Small differences in larval size might be accentuated in nature, due to improved performance under intracohort competition and predation (Frost 1954, Grimm & Klinge 1996). Even small differences in the larval size of pike may therefore have a high influence on the reproduction success of an individual female. However, the importance of maternal effect in the wild is not fully understood, as it is strongly linked with environmental factors and density-dependent life-history traits (Robertsen et al. 2013, Pagel et al. 2015, Vindenes et al. 2016). Selection on the basis of egg or larval size can be complex and have small-scale temporal and spatial variability, e.g. in areas of low intraspecific competition, or in case of later emerging juveniles, the advantage of large size may not be as evident (Robertsen et al. 2013). Also, in their study on the western coast of the Baltic Sea in Sweden, Berggren et al. (2016) found genetic-driven divergence in reproduction investment (egg size vs. body size) between sympatric subpopulations of pike, likely as a response to difference in substrate material between spawning grounds. Therefore, the best option to ensure population persistence in the long-term is to retain diverse spawning stock with wide length and age ranges and high genetic variability.

6. CONCLUSION AND FUTURE ASPECTS

The studies of this thesis demonstrated that HSL -regulated fishing can be strongly recommended to maintain diverse and viable pike populations. HSL preserved population density, biomass and diverse size-structure (**I**), as well as high pike production and consumption by diverse sized pike (**II**), whereas in MLL those features were greatly degenerated. By protecting large fish, HSL is able to preserve the long-term productivity of the fish population, because fishing mortality is compensated by increased recruitment and growth (**II**). In addition, HSL maintains stability of pike production and consumption, and enables a

strong piscivore effect on the ecosystem (**II, III**). Based on the high quality and amount of reproductive products in large females, these are important for the reproduction of pike populations, which should be considered in fisheries management (**IV**). However, the maternal effect seems not to be as unambiguous in pike as it has been found to be in some other piscivores in temperate lakes, such as perch (Olin et al. 2012) and walleye (Venturelli et al. 2010).

As an apex predator and popular gamefish, pike plays a crucial role by controlling prey fish populations and providing wellbeing in the form of recreational fishing (Carlson 2016), thus producing ecosystem services (Holmlund & Hammer 1999, Liguete et al. 2013). In the majority of developed countries, pike fishing is motivated mainly by recreational, and usually, non-consumptive motives underlined by increasing popularity of catch and release fishing (Arlinghaus 2006, Cooke & Schramm 2007, FAO 2012). Catch and release is a proven method to maintain fish population and high-quality fishing under relatively high fishing pressure (Arlinghaus et al. 2007, Cooke & Schramm 2007). Pike fisheries can be managed by catch and release –based regulation, as pike is resistant to handling and exhibits low post-release mortality (Tomcko 1997, Stålhammar et al. 2014, **I**). HSL enables harvest of intermediate sized individuals, but protects large individuals for their ecological importance and for trophy fish. Thus HSL is a promising tool to manage pike populations in a way that minimizes ecosystem effects (Arlinghaus et al. 2010, Pierce 2010, Matsumura et al. 2011, Gwinn et al. 2015), while still allowing a moderate mortality of medium-sized pike for subsistence fishing or low mortality by catch and release fishing.

As our understanding of effects of fishing and other human-induced stressors on fish populations increases, it has become evident that more sustainable practices to manage recreational fisheries are needed. A major problem in recreational fishing arises from difficulty to control angler effort and harvest rate (Post 2003). An important future aspect is to develop stock-based regulation strategies, which may provide high yields, but with low evolutionary impacts (Arlinghaus et al. 2010, Matsumura et al. 2011, Vainikka et al. 2017). In **I**, some evidence of decline of large pike in both HSL-lakes was observed. This may indicate that our study employed an excessive harvest rate in relation to growth rate, and that adequate recruitment to protected threshold length over a longer time period was not guarenteed. Therefore, management of fish population has to be considered stock-specifically, and depending on the growth rate, maturation size and age, and the fishing pressure, as

also suggested by Arlinghaus et al. (2010), Gwinn et al. (2015) and Vainikka et al. (2017).

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Project KESKALA: Studies on Ecologically Sustainable Fishing

The capability of harvestable slot-length limit regulation in conserving large and old northern pike (*Esox lucius*)

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In this experimental fisheries regulation study, we compared the effects of size-selective fishing according to minimum length limit (MLL, 40 cm) or harvestable slot-length limit (HSL, 40–64.9 cm) on population density, biomass, size and age structures, and sex ratio of the northern pike (*Esox lucius*). Data were collected during the years 2006–2013 in four 2.1–13.8 ha pristine forest lakes in southern Finland. In lakes where MLL fishing was carried out, pike density, biomass and size structure showed greater negative responses than in lakes where HSL fishing was carried out: mean length and age decreased, and large pike (≥ 65 cm) disappeared in just four years. HSL fishing affected the pike to a lesser extent, and large pike remained in the lakes, which is considered an essential feature of sustainable fishing. However, the results suggest that the number of large pike may decrease even under the HSL fishing strategy if the growth rate is slow and fishing is intensive, due to the high possibility of fish being caught before reaching the length beyond the upper HSL limit.

Introduction

The northern pike (*Esox lucius*) is a widespread and abundant cool-water predatory fish in the northern hemisphere. Pike plays a profound role in the ecosystem, since it can regulate the amount and composition of its prey species, as well as its own populations due to its highly cannibalistic behaviour (Raat 1988, Craig 1996, Sharma and Borgstrom 2008, Harvey 2009). In addition to its ecological importance, the pike is also an important and popular target species in recreational fisheries in Europe and North America. The popularity of pike as a gamefish stems from its large size and ferocity in fighting when hooked, as well as high catchability due to its abundance and aggressive feeding (Pierce *et al.* 1995, Paukert *et al.* 2001). As a result, the pike is very vulnerable to recreational fishing (Mosindy *et al.* 1987, Pierce *et al.* 1995, Pierce and Tomcko 2003), and requires sustainable management (Arlinghaus *et al.* 2010, Pierce 2010, Carlson 2016).

In developed countries, recreational fishing is the main factor affecting freshwater fish populations in many waterbodies, but its role in stock decline has been neglected until quite recently (Post *et al.* 2002, Allan *et al.* 2005, Cooke and Cowx 2006, Lewin *et al.* 2006, Post 2013). According to Post *et al.* (2002) and Lewin *et al.*

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(2006), the effects of recreational fishing on fish stocks include decline in population densities and changes in species composition, size distribution and trophic interactions. Targeting large individuals may cause truncation of age- and size distributions of a fish population, resulting in smaller mean size of fish. Fisheries-induced changes in life-history traits were observed in numerous marine and freshwater species for decades (Rose *et al.* 2001, Conover *et al.* 2009), including decrease in size and earlier maturation in perch (*Perca fluviatilis*) (Pukk *et al.* 2013), pikeperch (*Sander lucioperca*) (Mustamäki *et al.* 2014, Kokkonen *et al.* 2015) and pike (Edeline *et al.* 2007, Arlinghaus *et al.* 2009, Matsumura *et al.* 2011). Removal of large individuals by fishing favours early maturation and slow growth at the expense of fast-growing phenotypes which maturate later (Post *et al.* 2003, Cooke and Cowx 2004, Edeline *et al.* 2007, van Wijk *et al.* 2013). Intensive fishing may also alter fish behaviour, since actively swimming and fearless individuals are more likely to be caught (Härkönen *et al.* 2014). As activity in foraging and speed of growth are related, fisheries-induced selection is likely to favour more cautious and passive fish. Size-selective fishing may also be sex-selective, because females that usually grow faster and maturate later are more vulnerable to size-selective fishing than males (Lewin *et al.* 2006, Horppila *et al.* 2011).

Large females are essential to the vitality of a pike population, as they have higher absolute fecundity than smaller females (Craig 1996) and their progeny is also of better quality (Wright and Shoesmith 1988, Billard 1996, Kotakorpi *et al.* 2013). Eggs and larvae produced by large females are larger in terms of dry weight (*see* Kotakorpi *et al.* 2013) and consequently energy reserves in the yolk sacks are also greater (Ojanguren *et al.* 1996). This makes the larvae more resilient to starvation in their early life, less vulnerable to predation (Perez and Munch 2010) and more capable to use various prey items (Mehner *et al.* 1998). However, favourable effects of female size on offspring quality are not fully confirmed by studies carried out in natural environments (Pagel *et al.* 2015). This is due to a variety of factors affecting reproduction success, including the size-dependent timing of spawning (Murry *et al.* 2008), or trade-offs between different life-history strategies, e.g. growth benefit gained by increased activity *vs.* increased risk for predation (Estlander and Nurminen 2014).

From a fisheries management perspective, the detrimental effects of size-selective fishing can be diminished by regulating fisheries, for example by setting length limits for harvestable individuals. The most traditional of these regulation options is the minimum length limit (henceforth MLL). However, other approaches may be used, including maximum length limit, a combination of maximum and minimum length limits known as harvestable slot length limit (henceforth HSL), and the inverse of HSL, known as protected slot length limit (Paukert 2001, Arlinghaus *et al.* 2010, Carlson 2016). Traditional fisheries theories encourage harvesting large and old individuals in order to obtain maximum yield (Arlinghaus *et al.* 2010). As a result, severe size and age truncation has been observed in many commercially- and recreationally-exploited fresh- and brackish-water fish species like pikeperch (Kokkonen *et al.* 2015), perch (Pukk *et al.* 2013) and pike (Edeline *et al.* 2007, Pierce 2010, Carlson 2016).

In Finland, recreational fishing is hugely popular. According to the national fisheries inquiry, 1.5 million people, ca. 27% of the population, practise recreational fishing at least once a year (Natural Resources Institute Finland 2015). Pike is, after perch, the second most important catch species in recreational fishing in Finland. The recreational pike catch totalled ca. 7200 tonnes in 2014, of which less than 20% is released alive. The majority of catch, ca. 6300 tonnes, are caught from inland waters (Natural Resources Institute Finland 2015). Despite the popularity of pike recreational fishing, which also includes extensive use of effective fishing gears such as gillnets, there is no regulation of pike fishing in Finland. As recreational fishing may affect pike population structure and abundance (Jolley *et al.* 2008), it has likely affected negatively pike populations in many waterbodies in Finland. However, the impacts of recreational fishing are poorly documented. To maintain vitality of pike populations, it is important to develop sustainable practices for pike fisheries and to minimize the impacts of recreational fishing.

In order to better understand the effects of exploitation on pike stocks, we conducted an 8-year experimental pike fishery study, in which we monitored population responses to size-selective fishing by applying MLL of 40 cm and HSL of 40–64.9 cm in four protected forest lakes in southern Finland. Although size-based regulations (including of pike) have been evaluated in other studies (Arlinghaus *et al.* 2010, Pierce 2010, Matsumura *et al.* 2011, Gwinn *et al.* 2015), studies based on data from natural environments are still rare. This study offered a rare opportunity for long-term monitoring of two length limit-based regulation strategies in experimental but still natural environment without external fishing. Our aim was to compare the responses of pike population size, biomass and size and age-structure, when subjected to intensive fishing under MLL or HSL regulation. Our hypotheses based on earlier studies (Arlinghaus *et al.* 2010, Pierce 2010, Matsumura *et al.* 2011, Gwinn *et al.* 2015) were:

1. Pike density and especially biomass would decrease in MLL lakes, whereas in HSL lakes these parameters would be less affected due to conservation of large individuals.
2. Pike population structure would shift towards smaller and younger individuals in MLL lakes, while in HSL lakes large and old individuals remain in the population.
3. Female-to-male ratio would shift towards male dominance in MLL lakes, because females are more vulnerable to fishing. In HSL lakes the sex ratio would remain constant as large individuals (which are often female) are conserved.

Material and methods

Study lakes

The study was conducted in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi which are small forest lakes in Hämeenlinna (southern Finland, 61°13´N, 25°12´E) during the years 2006–2013. Surface areas of the lakes are 13.8, 2.1, 8.4 and 3.4 ha, mean depths 6.1, 3.8, 2.2 and 4.6 m and maximum depths 12.0, 8.0, 6.0 and 12.0 m, respectively (Horppila *et al.* 2010). The lakes are nearly pristine, oligo-mesotrophic, and colored by humic substances. Mean water colour is 130 and 150 mg Pt l^{-1} in the less humic Hokajärvi and Haarajärvi, respectively, and 330 and 340 mg Pt l^{-1} in the more humic Haukijärvi and Majajärvi, respectively (Horppila *et al.* 2010). The lakes are not subjected to agricultural or industrial pollution, they are reserved for research use only, and recreational or professional fishing is not allowed. The lakes have strong temperature stratification, and subsequently display hypoxia in the hypolimnion, during both summer and winter. The sole exception is Haarajärvi, where the hypolimnion is well oxygenated throughout the year. Due to low euphotic depth and steep banks, the littoral vegetation zone is narrow (coverage 4%–15%), resulting in limited habitats for pike, except in Hokajärvi (littoral vegetation coverage 80%). Although the aforementioned conditions are normal for small humic lakes (Rask *et al.* 1999), they have profound effects on fish communities, restricting the species number and regulating species interactions (Olin *et al.* 2010). In all the lakes the dominating fish species are perch, roach (*Rutilus rutilus*) and pike. Other species include bream (*Abramis brama*) and bleak (*Alburnus alburnus*) in Hokajärvi and Haukijärvi, burbot (*Lota lota*) in Haarajärvi, Haukijärvi and Hokajärvi, as well as introduced whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in Haarajärvi and tench (*Tinca tinca*) in Majajärvi (Olin *et al.* 2010).

Mark and recapture and pike removal

Pike population densities, biomass and size structures were determined using a capture-mark-recapture program in years 2006–2013 (Table 1). Multigear sampling was used to minimize the effect of gear selectivity and to increase catch and improve coverage. Fyke nets and wire traps were used during and after the spawning time of pike (late April to early–mid-May), starting immediately after ice melting and continuing 2–3 weeks. Fyke nets were placed in the spawning grounds of pike, and wire traps were placed evenly along the shoreline. During summer and autumn, pike were caught by gill-

nets and angling. As part of the standard experimental gillnet fishing program (CEN 2005) in the study lakes, Nordic multimesh gillnets (mesh size 5–55 mm) with stratified random sampling were used annually three times in July–August (Olin *et al.* 2010). When necessary to fulfil the target catch, additional gillnetting with 2 × 30 m gillnets of 45–60 mm mesh size was conducted in late autumn. Intensive angling was conducted annually between late August and early September, in which the whole littoral area was sampled at least four times during different days and times using a rowboat with 1–2 anglers. A variety of commonly used artificial lures, 5–12 cm in size, were applied: wobblers, jerkbaits, softbaits, spoons and spinners, but also live baitfish were occasionally used. Additional angling (on average three times per year per lake) was conducted alongside other sampling with the same methods as described above.

Pike of ≥ 30 cm were tagged with individually-coded Carlin tags in 2006 and Floy T-bar anchor tags in 2007–2013. Both types of tags were inserted into muscle tissue at the base of the dorsal fin. Pike of < 30 cm were not tagged due to assumed higher post-release mortality of these individuals. All pike were marked by finclipping (right or left pelvic fin depending on the year) in order to control the loss of individual tags. Tagged pike were kept for ca. 10 minutes in a large tub filled with water before releasing to determine the survival rate after handling. Severely injured pike and individuals included in the removal catch were immediately killed after being caught.

To compare pike population responses to fishing according to MLL and HSL regulations, pike populations in the four study lakes were subjected to two different size-selective removal procedures during 2008–2012: MLL of ≥ 40 cm in Hokajärvi and Majajärvi, and HSL of 40–64.9 cm in Haarajärvi and Haukijärvi. Target catch was 50% of the estimated spring biomass of ≥40 cm or 40–64.9 cm pike in MLL or HSL lakes, respectively. The MLL of 40 cm was selected, because this value roughly equals female pike maturation size in all study lakes. This size was also MLL for pike in Finland until 1993. The maximum length limit of 65 cm in HSL lakes was selected to ensure a reasonable

Table 1. Total numbers of pike caught, new and previously marked individuals (IDs) and total numbers of marked pike in autumn 2006 and in spring 2007–2013. Pike marking started in spring 2006. 'Total marked' values include numbers of individuals tagged in earlier years corrected with natural mortality estimates. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2006	2007	2008	2009	2010	2011	2012	2013
Haarajärvi (HSL)								
Total catch	44	62	82	80	55	32	52	38
New ID	38	45	50	36	25	12	26	23
Prev. ID	6	17	32	44	30	20	26	15
Total marked	57.0	50.6	90.7	131.8	112.6	92.0	71.7	61.0
Haukijärvi (HSL)								
Total catch	11	5	8	2	7	3	6	7
New ID	4	2	2	0	3	2	2	4
Prev. ID	7	3	6	2	4	1	4	3
Total marked	13.0	12.2	14.0	9.7	5.5	5.9	4.8	6.6
Hokajärvi (MLL)								
Total catch	17	14	31	37	31	31	36	25
New ID	10	9	22	26	22	22	26	16
Prev. ID	7	5	9	11	9	9	10	9
Total marked	40.0	32.0	35.0	34.7	23.1	21.2	25.2	30.6
Majajärvi (MLL)								
Total catch	19	17	26	18	5	9	12	8
New ID	2	6	12	7	3	5	4	4
Prev. ID	17	11	14	11	2	4	8	4
Total marked	46.0	34.1	35.6	33.9	15.9	13.3	11.2	5.2

number of pike also in the largest size class (≥ 5% of the total population). The rationale to compare (relatively low) MLL and HSL was to compare responses of "traditional" MLL-based regulation and HSL regulation where large pike are conserved.

Population density, biomass and size and age-structure estimations

Population size estimates for tag-marked ≥ 35 cm pike were calculated for autumn 2006 and spring 2007–2013. Spring estimates had higher number of individuals as compared with the autumn estimates, and were used when possible. In 2006, the first pike were tagged in spring and thus only an autumn population estimate was possible. A modified Petersen method (Chapman version, Seber 1982: 60) was used to calculate pike population size in year t (N_t) by using following equation:

$$N_t = \frac{\left\{\left[\left(\sum_{t_0}^{t_{n-1}} T_{\geq 35\,\mathrm{cm}} S\right)+1\right](n+1)\right\}}{(m+1)-1} \quad (1),$$

where t_0 and t_n are the first and the latest tagging year, $T_{\geq 35\mathrm{cm}}$ is the total number of ≥ 35 cm tagged pike, S is the yearly survival rate, n is the sample size, and m is the number of marked fish in a sample. Since m/n ratios and sample sizes varied considerably among lakes and years, the upper and lower boundaries of 95% confidence limit interval were calculated by Poisson or binomial distribution as suggested by Seber (1982). As there was 0.5–1 year delay between tagging and recapturing and apparent recruitment to the catchable population during that time, the new recruits were excluded from the Petersen estimates by including only ≥ 35 cm pike in n and m (yearly length increment of 30–35 cm individuals was on average 5 cm) and by excluding 30–34.9 cm individuals tagged in preceding autumn from $T_{\geq 35\mathrm{cm}}$ in next spring. Pike biomass was calculated using population density estimates, length distributions and lake-specific length-mass power regression equations, which were $m = 0.005L^{3.0183}$ ($r^2 = 0.9792$) for Haarajärvi, $m = 0.0037L^{3.1168}$ ($r^2 = 0.991$) for Haukijärvi, $m = 0.0037L^{3.1127}$ ($r^2 = 0.9837$) for Hokajärvi and $m = 0.0043L^{3.0862}$ ($r^2 = 0.9915$) for Majajärvi, in which m = estimated mass (g), L total length (mm) and r^2 is the coefficient of determination describing the fit.

All pike were measured to the nearest 1 mm (total length). Removed pike and released large (≥ 65 cm) individuals were weighed to the nearest 1 g and 10 g, respectively. All individuals caught within a year were included in spring length distributions either by using their direct lengths (before the onset of growth) or estimated spring lengths (by subtracting estimated plus-growth based on back-calculated growth analyses). Sex of ripe individuals was determined by running reproductive products at spawning time, or from gonad preparation in cases when pike were killed. Age and back-calculated growth were determined by one experienced reader either from scales from released pike (n = 521) or cleithrum bones from removed pike (n = 728) using a Fraser-Lee equation (Frost and Kipling 1959) or a linear growth model (Casselman 1990). For the yearly age distributions, observed age for the aged individuals was used and for other individuals the age was estimated by using age-length keys based on back-calculated length at age data as described in Horppila *et al.* (2010). The pooled age distributions in 2006–2008 were used to estimate total mortality (Z) by the catch-curve method (Robson and Chapman 1961). The first fully-recruited age group was 4 yr. except in Haukijärvi, where the catch-curve could be fitted only to the catch of ≥ 9-yr. individuals. Z was estimated to be 0.21, 0.32, 0.27 and 0.23 in Haukijärvi, Majajärvi, Hokajärvi and Haarajärvi, respectively, and the corresponding r^2 values were 0.738, 0.852, 0.901 and 0.947. Annual mortality (A) was calculated as $A = 1 - e^{-Z}$, and $S = 1 - A$. Natural mortality (M) was assumed to be equal to total mortality (Z) in 2006–2008, i.e., before pike removal affected the demographic structure.

Statistical analyses

To detect changes in pike population structure, the year-to-year differences in frequencies of the size classes S (small = 30.0–39.9 cm), M (medium = 40.0–64.9 cm) and L (large

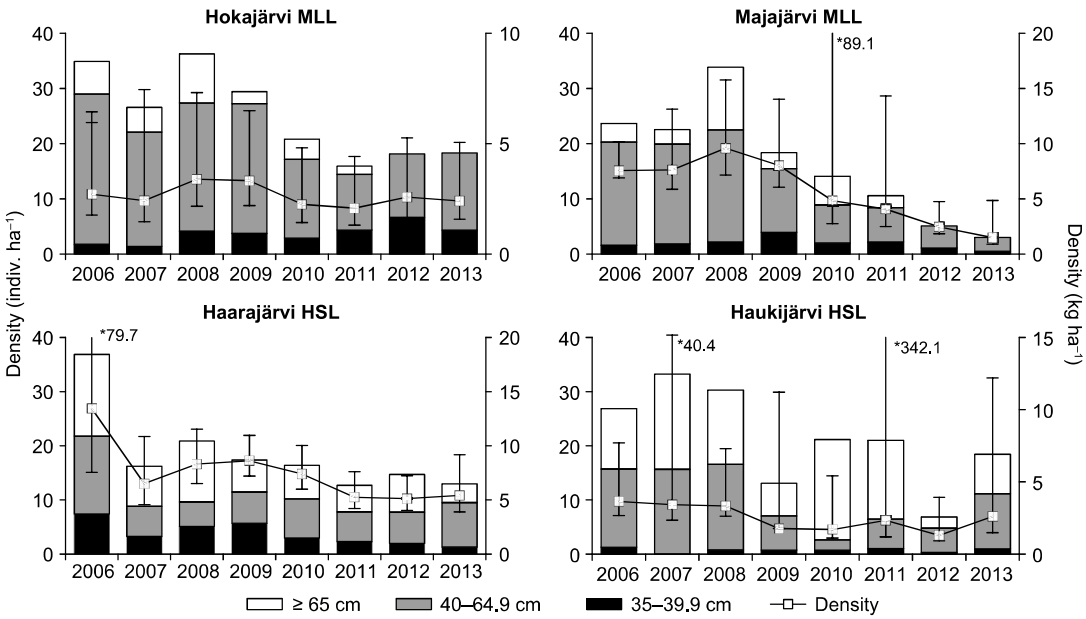

Fig. 1. Pike density estimates with 95% confidence limits and biomass estimates (columns) with proportions of 35–39.9 cm, 40–64.9 cm and ≥ 65 cm pike in research lakes in years 2006–2013. MLL = Minimum length limit, HSL = Harvestable slot-length limit. Removal fishing of pike ≥ 40 (MLL) or 40–64.9 cm (HSL) was conducted in 2008–2012.

≥ 65.0 cm), as well as female and male frequencies of pike were calculated by Fisher's exact test. Tests were conducted for each lake separately. Between-year differences were further examined by pairwise comparisons (Fisher's exact test) with the Bonferroni correction for multiple comparisons. Only pike of ≥ 30 cm total length were used in all statistical calculations, as this was the length threshold for tagging. In addition, our catching methods (spawning-time trapping, angling) for pike were poorly suitable for < 30 cm pike. The analyses were performed using R ver. 3.1.0.

A general linear model was applied to the data from each lake to investigate trends in pike population density, biomass and mean length and age, in response to HSL and MLL regulation in 2006–2013. In case of Haarajärvi, the year 2006 was excluded from density and biomass analyses, as the density estimate for 2006 was almost two times higher (with wide 95% confidence limits) than the estimates for 2007 and 2008, and thus considered not representative of initial pike population before the start of removal fishing. The above analysis was performed using SAS ver. 9.4.

Results

Pre-treatment conditions

Prior to pike removal experiment, pike average density estimates for 2006–2008 (except in Haarajärvi 2007–2008) were 14.8 and 9.2 indiv. ha^{-1} in HSL-lakes Haarajärvi and Haukijärvi, respectively, and 11.4 and 16.5 indiv. ha^{-1} in MLL-lakes Hokajärvi and Majajärvi, respectively (Fig. 1). Corresponding average biomass estimates were 9.3, 11.3, 8.1 and 13.3 kg ha^{-1} in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively. In each of the study lakes all size classes (S, M and L) were present (Fig. 1). Large pike (≥ 65 cm) comprised on average 12.8% and 46.8% of the estimated total density and biomass, respectively, in Haarajärvi; 21.9% and 46.6%, respectively, in Haukijärvi; 7.2% and 19.4%, respectively, in Hokajärvi; and 5.5% and 19.8%, respectively, in Majajärvi. Pike average lengths (2006–2008 average) were 42.7, 53.0, 46.7 and 45.3 cm, average ages 7.0, 9.2, 7.4 and 6.7 years and female percentages 40.7%, 45.0%, 46.%8 and 39.4% in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively.

Pike removal catches

Pike removal catch during 2008–2012 in HSL lakes (Table 2) totalled 309 individuals and 150 kg (2.0–2.5 kg ha^{-1} yr^{-1}) and 32 individuals and 26 kg (1.9–3.6 kg ha^{-1} yr^{-1}) in Haarajärvi and Haukijärvi, respectively. In MLL lakes, Hokajärvi and Majajärvi, the corresponding numbers were 204 individuals and 123 kg (2.0–3.8 kg ha^{-1} yr^{-1}) and 108 individuals and 76 kg (3.5–5.9 kg ha^{-1} yr^{-1}). The removal catch by weight, which was set up by spring biomass estimates, declined clearly in MLL lakes during the removal years but in HSL lakes it either fluctuated (Haukijärvi) or remained quite stable (Haarajärvi) reflecting the changes in or stability of the estimated total biomass (Table 2 and Fig. s1).

Pike average removal percentages (and ranges) of the estimated total biomass (H_b) in 2008–2012 were higher in MLL lakes Hokajärvi (50.1%, 39.6%–57.3%) and Majajärvi (73.2%, 34.6%–137%) than in HSL lakes Haarajärvi (27%, 22.6%–35.5%) and Haukijärvi (47.1%, 23.8%–83.8%). The percentages of the removed numbers of individuals (H_n) differed less clearly between treatments. In MLL lakes, Majajärvi and Hokajärvi, average H_n in removal years (2008–2012) were 60.4% and 39.6%, respectively, and in HSL lakes, Haukijärvi and Haarajärvi, 54.7% and 31.6%, respectively. The H_n values for medium sized pike (40–64.9 cm) in the removal years were almost identical between the treatments: 68.6% and 48.3% in MLL lakes Majajärvi and Hokajärvi, respectively, and 71.9% and 46.7% in HSL lakes Haukijärvi and Haarajärvi, respectively.

Responses in population density and biomass

Estimated pike population abundances decreased significantly in both MLL lakes (Fig. 1 and Table 3). In Majajärvi, both estimated density and biomass decreased (by 82.0% and 88.7%, respectively, from 2006–2008 to 2013). In Hokajärvi, estimated biomass decreased significantly

Table 2. Annual pike removals from study lakes in 2008–2012 including numbers and weights removed per hectare, and removal percentages of estimated biomass removed (≥ 40 or 40–64.9 cm individuals), and percentages of females in removal catch. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2008	2009	2010	2011	2012
Haarajärvi (HSL)					
Removal (indiv. ha^{-1})	4.9	4.3	4.6	4.6	4.0
Removal (kg ha^{-1})	2.5	2.0	2.0	2.3	2.1
Removal (% of biomass)	24.3	22.6	24.7	35.5	27.9
Removed females (%)	55	37	59	50	37
Haukijärvi (HSL)					
Removal (indiv. ha^{-1})	2.9	4.9	1.9	2.4	3.4
Removal (kg ha^{-1})	2.7	3.6	1.9	2.5	2.2
Removal (% of biomass)	23.8	72.5	23.8	31.7	83.8
Removed females (%)	0	50	50	25	57
Hokajärvi (MLL)					
Removal (indiv. ha^{-1})	4.3	7.1	4.6	3.6	4.6
Removal (kg ha^{-1})	3.6	3.8	3.0	2.0	2.3
Removal (% of biomass)	39.6	54.0	57.3	49.3	50.5
Removed females (%)	65	58	63	53	63
Majajärvi (MLL)					
Removal (indiv. ha^{-1})	7.7	7.1	4.4	6.5	6.2
Removal (kg ha^{-1})	5.9	4.4	4.0	4.7	3.5
Removal (% of biomass)	34.6	47.5	57.4	89.4	137.0*
Removed females (%)	38	70	60	37	50

* Removal catch in 2012 exceeded estimated biomass.

(by 43.7%), but the 15.2% decrease in density was statistically insignificant. In HSL lakes, estimated density and biomass decreased only little, and not significantly, in the course of the study (Fig. 1 and Table 3). In Haarajärvi, density and biomass estimates for 2013 were 26.7% and 30.1% lower than the average level in 2006–2008. In Haukijärvi, the between-year variation was high during the study (Fig. 1), but the density and biomass estimates for 2013 were respectively 25.1% and 38.8% lower as compared with those for the pre-treatment levels.

Responses in population structure, age and sex distribution

Mean length of pike decreased significantly in both MLL lakes (Table 3), the decrease being 9.5% in Hokajärvi and 6.8% in Majajärvi towards the end of the experiment (Table 4). In HSL lakes, Haarajärvi and Haukijärvi, no significant changes in mean length were detected (Table 3). In HSL lakes, large (≥ 65 cm) pike that were released comprised a substantial part of the total biomass (Haarajärvi 26.8%–53.8%; Haukijärvi 30.2%–87.6%) during the study period, indi-

Table 3. Development of pike density, biomass, mean length and age in 2006–2013 analysed by general linear model. Significant values of the effect of year are set in boldface. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	Effect	Estimate	SE	df	*t*	*p*
Haarajärvi (HSL)						
Density	Intercept	17.941	2.399	5	7.48	0.0007
	Year	–0.926	0.446	5	–2.08	0.0924
Biomass	Intercept	10.335	1.064	5	9.71	0.0002
	Year	–0.478	0.198	5	–2.42	0.0602
Mean length	Intercept	41.758	0.953	6	43.83	< 0.0001
	Year	0.277	0.189	6	1.47	0.1928
Mean age	Intercept	7.4009	0.4877	6	15.17	< 0.0001
	Year	–0.0726	0.09658	6	–0.75	0.4807
Haukijärvi (HSL)						
Density	Intercept	9.707	1.436	6	6.76	0.0005
	Year	–0.667	0.284	6	–2.35	0.0573
Biomass	Intercept	12.247	1.977	6	6.19	0.0008
	Year	–0.941	0.392	6	–2.40	0.053
Mean length	Intercept	55.423	3.534	6	15.68	< 0.0001
	Year	–0.835	0.700	6	–1.19	0.2777
Mean age	Intercept	10.2383	1.035	6	9.89	< 0.0001
	Year	–0.4254	0.205	6	–2.08	0.0833
Hokajärvi (MLL)						
Density	Intercept	11.937	1.493	6	8.00	0.0002
	Year	–0.299	0.296	6	–1.01	0.3507
Biomass	Intercept	9.240	0.878	6	10.53	< 0.0001
	Year	–0.673	0.174	6	–3.87	**0.0083**
Mean length	Intercept	48.325	1.256	6	38.47	< 0.0001
	Year	–1.081	0.249	6	–4.34	**0.0049**
Mean age	Intercept	7.6899	0.27	6	28.48	< 0.0001
	Year	–0.1752	0.05347	6	–3.28	**0.0169**
Majajärvi (MLL)						
Density	Intercept	20.862	2.304	6	9.06	0.0001
	Year	–2.098	0.456	6	–4.60	**0.0037**
Biomass	Intercept	16.394	2.181	6	7.52	0.0003
	Year	–1.821	0.432	6	–4.21	**0.0056**
Mean length	Intercept	46.417	0.805	6	57.68	< 0.0001
	Year	–0.691	0.159	6	–4.33	**0.0049**
Mean age	Intercept	7.2631	0.1846	6	39.34	< 0.0001
	Year	–0.198	0.03656	6	–5.42	**0.0016**

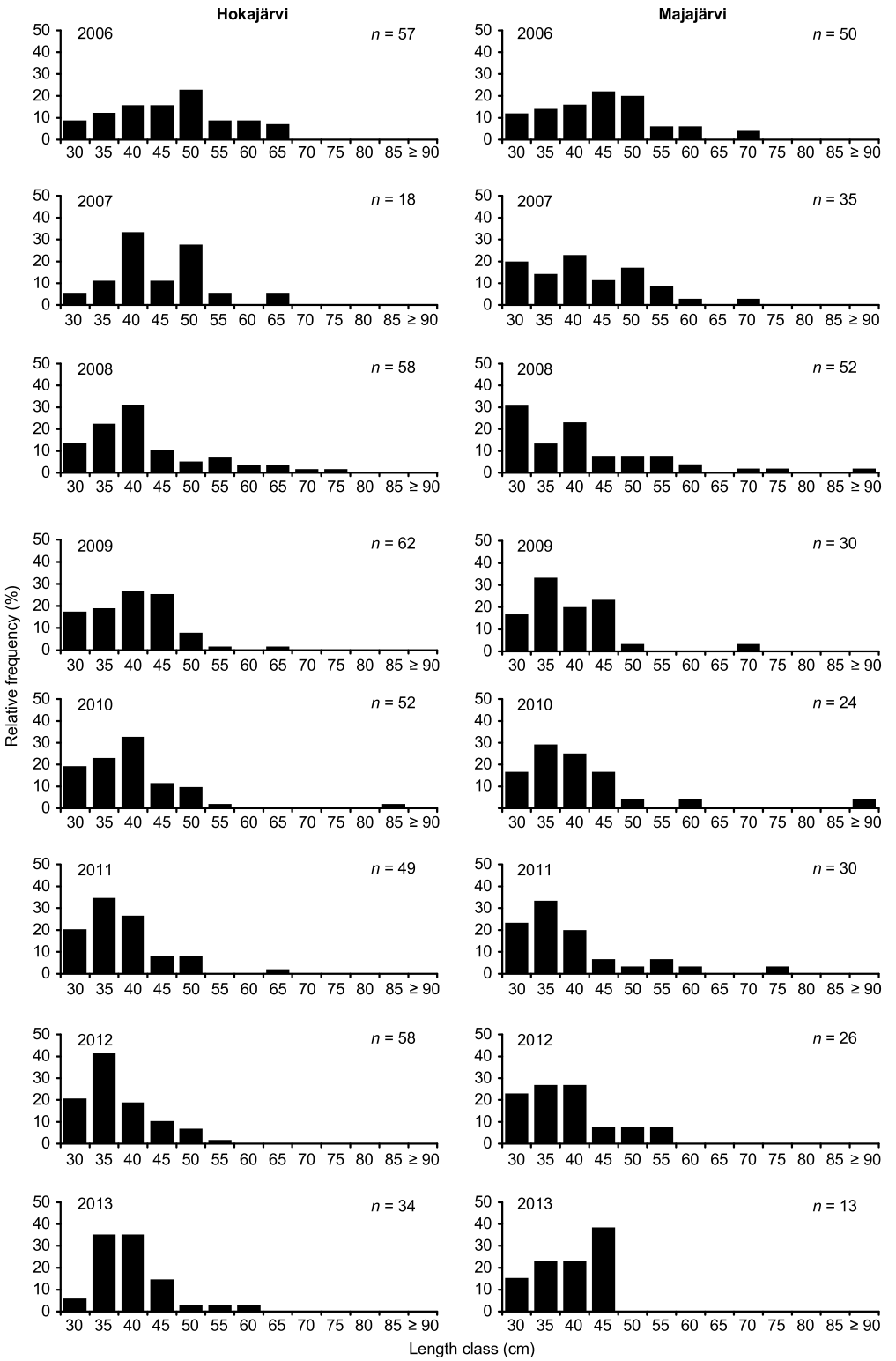

Fig. 2. Pike length frequency distributions in MLL-lakes in spring in years 2006–2013. Removal fishing of pike ≥ 40 cm was conducted in 2008–2012.

cating low mortality due to handling. Large pike disappeared completely from both MLL lakes four years after the start of pike removal (Figs. 1 and 2). In MLL lake Hokajärvi, removal gradually led to the dominance of < 45 cm pike (Fig. 2). This was evidenced by significant differences in annual frequencies of S, M and L size classes (Table 4) between pre-removal and "late removal" years. For example, the frequencies in 2006 differed from the frequencies in 2011 and 2012; and the frequencies in 2007 from the frequencies in 2011 (Fisher's exact test: p = 0.020, < 0.001 and 0.019, respectively). In the other MLL lake (Majajärvi), length distributions in the years 2012 and 2013 were severely truncated as compared with those in the years before pike removal (Fig. 2). However, the differences between the annual frequencies of size-classes S, M and L were not significant (Fisher's exact test: $p > 0.05$), as truncation took place within the medium size-class. In HSL lake Haarajärvi, intensive fishing of M-sized pike did not prevent high recruitment to harvestable size. In 2013 the frequency of M-sized pike (40–64.9 cm) was the highest in the study period (60.4%, Table 4), and differed significantly from the frequencies in 2006, 2008 and 2009 (Fisher's exact test: p = 0.0064, < 0.001 and 0.001, respectively). The size-structure distribution remained rather unchanged during the study as either 35–39.9 cm or 40–44.9 cm pike dominated every year (Fig. 3). In the other HSL lake (Haukijärvi), the

Table 4. Total numbers of ≥ 30 cm pike caught, female percentages, mean lengths and weights, and frequencies of small (S), medium (M) and large (L) pike in the study lakes in the years 2006–2013. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	2006	2007	2008	2009	2010	2011	2012	2013
Haarajärvi (HSL)								
≥ 30 cm pike caught	111	90	179	122	112	103	97	53
Female (%)	44.4	35.5	42.2	36.4	49.5	42.2	33.8	45.2
Mean length (cm)	43.4	43.0	41.6	40.8	42.8	43.3	44.6	44.5
Mean weigth (g)	577	557	515	453	514	534	636	559
S, 30–39.9 cm (%)	60.4	53.3	68.7	65.6	43.8	50.5	48.5	34.0
M, 40–64.9 cm (%)	30.6	36.7	21.2	28.7	48.2	40.8	40.2	60.4
L, ≥ 65 cm (%)	9.0	10.0	10.1	5.7	8.0	8.7	11.3	5.7
Haukijärvi (HSL)								
≥ 30 cm pike caught	20	12	12	12	10	10	15	17
Female (%)	38.5	66.7	30.0	54.5	70.0	40.0	55.6	81.8
Mean length (cm)	51.5	54.8	52.5	50.5	59.7	52.3	43.7	48.2
Mean weigth (g)	994	1172	1095	962	1746	1264	584	904
S, 30–39.9 cm (%)	20.0	16.7	25.0	33.3	20.0	20.0	53.3	29.4
M, 40–64.9 (%)	65.0	58.3	58.3	50.0	30.0	60.0	40.0	64.7
L, ≥ 65 cm (%)	15.0	25.0	16.7	16.7	50.0	20.0	6.7	5.9
Hokajärvi (MLL)								
≥ 30 cm pike caught	57	21	61	63	56	51	58	36
Female (%)	37.5	41.7	61.4	63.3	59.2	40.0	48.1	42.4
Mean length (cm)	48.5	47.2	44.5	42.3	42.1	40.6	40.1	42.3
Mean weigth (g)	751	660	598	490	502	421	390	461
S, 30–39.9 cm (%)	21.1	28.6	39.3	36.5	46.4	56.9	62.1	44.4
M, 40–64.9 cm (%)	71.9	66.7	54.1	61.9	51.8	41.2	37.9	55.6
L, ≥ 65 cm (%)	7.0	4.8	6.6	1.6	1.8	2.0	0	0
Majajärvi (MLL)								
≥ 30 cm pike caught	50	36	54	30	24	32	26	15
Female (%)	33.3	45.5	39.5	60.7	47.6	39.3	40.0	26.7
Mean length (cm)	47.0	45.1	43.8	42.1	43.0	42.2	41.1	42.2
Mean weigth (g)	713.2	631.2	670.3	516.2	640.2	548.0	445.8	466.8
S, 30–39.9 cm (%)	26.0	36.1	45.3	50.0	45.8	59.4	50.0	46.7
M, 40–64.9 cm (%)	70.0	61.1	49.1	46.7	50.0	37.5	50.0	53.3
L, ≥ 65 cm (%)	4.0	2.8	5.7	3.3	4.2	3.1	0	0

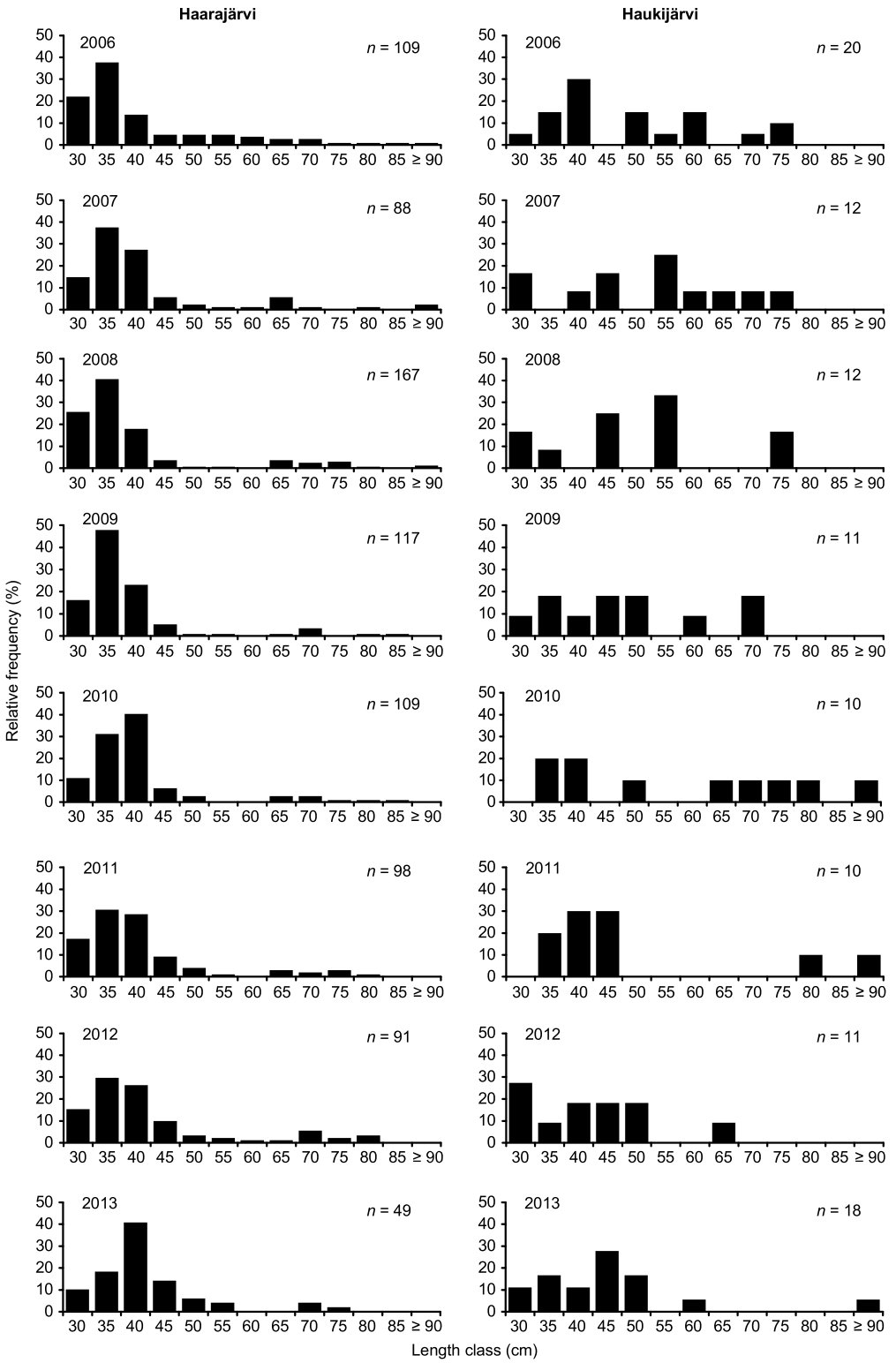

Fig. 3. Pike length frequency distributions in HSL-lakes in spring in years 2006–2013. Removal fishing of pike 40–64.9 cm was conducted in 2008–2012.

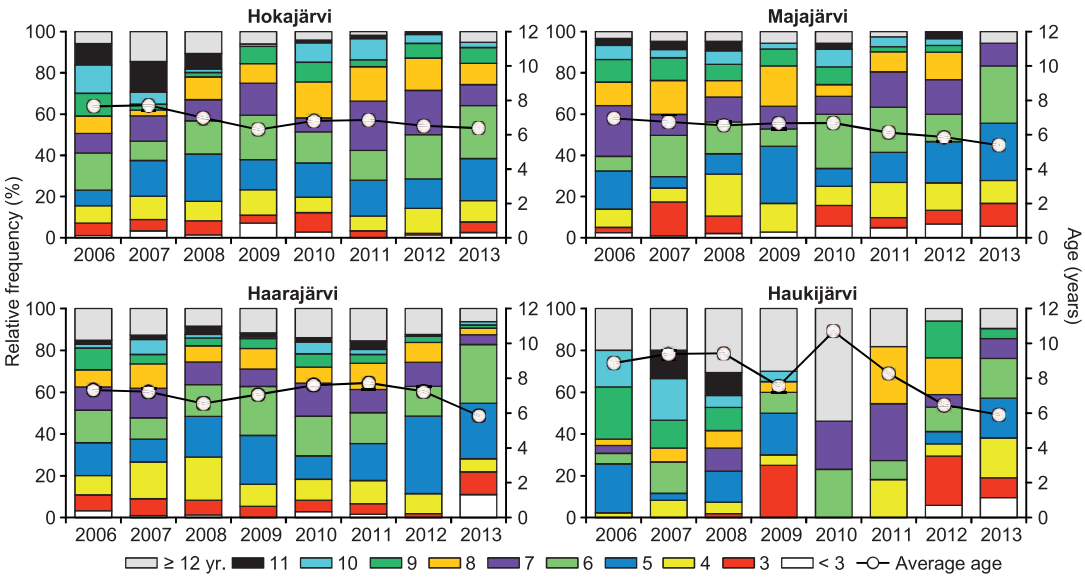

Fig. 4. Pike age distribution and average age in study lakes in 2006–2013.

frequencies of S-, M- and L-sized pike fluctuated between years (Fig. 3 and Table 4), and there was no significant response to removal (Fisher's exact test: $p > 0.05$).

The average age of pike decreased significantly during the course of the study in both MLL lakes (Hokajärvi and Majajärvi; Fig. 4 and Table 3). From 2006–2008 (average) to 2013, the average age decreased from 7.4 to 6.4 years (14.3%) in Hokajärvi and from 6.7 to 5.5 years (20.2%) in Majajärvi. In HSL lakes Haarajärvi and Haukijärvi, no decrease was detected, as in Haarajärvi the mean age was quite consistently between 6.6 and 7.7 years in 2006–2012, being the lowest (5.9 years) in 2013; and the pike mean age in Haukijärvi fluctuated considerably, being the highest (10.7 years) in 2010 and lowest (5.9 years) in 2013 (Fig. 4). The pike populations in all the lakes consisted of several age classes but the share of younger age classes (especially < 3 years) increased during the study period indicating increased recruitment (Fig. 4). Interestingly, large pike (≥ 65 cm; average age 13.5, 12.2, 11.7 and 12.9 years of age in Hokajärvi, Majajärvi, Haukijärvi and Haarajärvi, respectively) disappeared completely from the MLL lakes, but smaller pike of comparable age remained in the populations until the end of the study.

Average female percentages during the study were 41.2%, 54.6%, 49.2% and 41.6%, in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Table 4). Contrary to our hypotheses, there were no significant changes in female-to-male ratio in any of the lakes during the study years (Fisher's exact test: $p > 0.05$), although female percentages in removal catches were higher than female percentages in total catches, except in Haukijärvi (Tables 2 and 4).

Discussion

Responses of pike population to size selective fishing by HSL or MLL

According to our study, HSL regulation retained large pike in the lakes and maintained pike population abundance close to the original levels despite, which is considered an essential feature in sustainable fishing (Arlinghaus *et al.* 2010, Gwinn *et al.* 2015). In contrast, the abundance of large individuals decreased rapidly in the MLL lakes and large pike vanished in just four years. Our study supports earlier studies (Snow and Beard 1972, Kempinger and Carline 1978, Pierce *et al.* 1995, Arlinghaus *et al.* 2010, Pierce 2010) criticizing MLL fishing (especially if the

threshold length is set too low) as being unable to maintain either pike fishery yield or diverse size-structure for conservational purpose. Our results also concur with the meta-analysis by Pierce (2010), that implementation of maximum size-limits improves population size structure in terms of presence of large pike, but has less effect on population density as compared with lakes where MLL was applied. In both MLL lakes, the biomass response was more evident than the response in density, which is logical as the biomass estimate is affected not only by density, but also by size structure, and the catchability of large individuals seemed to be higher than that of smaller ones.

The study revealed that pike populations in different lakes may respond differently to similar size-selective fishing. Pike populations responded differently (but in both cases negatively) to MLL regulation in Majajärvi and Hokajärvi. In Majajärvi, both pike density and biomass collapsed, while mean size decreased, and size structure was truncated. In Hokajärvi, pike density decreased only little, but biomass almost halved, as size structure was truncated and mean size decreased. Truncation of the size distribution was also evidenced by changes in frequencies of S-, M- and L-sized pike between pre-removal and late removal years in Hokajärvi, but in Majajärvi changes in frequencies of size-classes were not found, as the number of large pike was low, and truncation took place within medium size-class. Differences in population-density responses between Hokajärvi and Majajärvi are likely explained by considerably greater removal percentage in Majajärvi in 2011 and 2012, which led to a collapse of the pike population. Also, the lake morphology features such as small size, steep banks, narrow euphotic layer and consequently narrow vegetated zone may have contributed to the population decline in Majajärvi, as pike were observed to gather along the shoreline where they are easily caught. Furthermore, the large vegetated littoral areas in Hokajärvi may have contributed to effective reproduction and compensatory recruitment of small pike (Bry 1996), which may partly explain why pike density was less affected in Hokajärvi.

HSL regulation seemed to be more sustainable than MLL, as there were no decrease (although quite close) in either lake in population density, biomass and mean size, and large pike remained in populations until the end of the study. Changes in frequencies of S-, M- and L-sized pike expressed increased recruitment and growth in Haarajärvi, indicating that HSL regulation would not have decreased population abundance even if the experiment was continued. The pike size structure in Haukijärvi practically did not change, but these results are quite difficult to interpret, as the length distribution showed high year-to-year fluctuation, which is likely due to small sample size. Small populations are also prone to high between-year variation due to environmental and demographic stochasticity (Lande 1993).

Our study also indicated that the age structure of the pike population may be less affected by fishing than the size structure. Although mean length and age decreased, large pike vanished and size distributions were severely truncated in both MLL-regulated lakes, the effect on age distribution was not as evident as compared with variations in the size structure. Old (≥ 12 years) pike remained to some extent in Hokajärvi and Majajärvi until end of the study. This finding implies that even though large individuals were not especially targeted in the MLL lakes, they were vulnerable to fishing as Pierce and Tomcko (2003) have suggested, indicating that fishing was positively size-selective, favouring slow-growing and passive individuals at the expense of fast-growing and actively-feeding ones. This may have an adverse effect on pike population productivity via genetic selection, as the share of fast growing genotypes decreases in the population (Cook and Younk 1998, Lewin *et al.* 2006). According to our study, HSL regulation will reduce the risk of positively size-selective fishing. Therefore, we concur with the results of recent studies (Arlinghaus *et al.* 2010, Pierce 2010) that recommend protection of large pike, whose higher energy need and activity increases their probability of being caught in recreational fishing (Lewin *et al.* 2006, Pierce and Tomcko 2003).

MLL regulation should decrease the number of female pike more than that of male pike, as large pike are more likely to be females whose probability to be caught under this regime is high (Craig 1996, Lewin *et al.* 2006). This was found

in our study as well, as more females than males were included in the removal catch. However, female-to-male ratio did not shift towards male dominance even in the MLL lakes, where large individuals were targeted. Due to the higher catchability of females, they may have been overrepresented in the pike density data which in turn masked the possible reduction in the share of females in the populations. Another explanation could be earlier maturation of females due to faster growth (first author's unpubl. data) which increased their relative abundance in recruiting year-classes as was observed for perch (Olin *et al.* 2017). However, our sex-distribution data on young pike was too scarce to verify this. In the long run, female-selective fishing is documented to have detrimental effects on recruitment (Lewin *et al.* 2006).

Reliability of the results

The advantage of HSL over MLL in this study could be partly explained by smaller removal percentage of biomass as a result of release of large individuals, which, despite their small number, comprised a large share of the pike biomass. However, when considering removal percentages of removed numbers, the difference was less obvious, and removal percentages of medium-sized pike (40–64.9 cm) were almost identical between the treatments. At the end of the experiment, when large pike had completely vanished from both MLL lakes and removal catch consisted almost solely of medium-sized pike, the main difference between the treatments was the release of large pike in HSL lakes, and not the contrasting harvest rates between the fishing regimes. Our study indicates how MLL and HSL would work in practical fisheries management in situations where fish population with initially low (or zero) harvest rate faces sudden increase in fishing pressure. In this scenario, initially high kept catch in MLL lakes would decrease eventually to the levels of HSL lakes but the size structure under HSL would be more diverse including large individuals and fishing is thus more sustainable. In the long run, HSL lakes may continue producing relatively high harvests, as large individuals are able to spawn and produce strong year-classes, whereas in MLL lakes the reproductive potential of the small-sized spawning stock is lower and the catch would probably decrease further.

As our population density and biomass estimates were based on mark-recapture data, we followed the prerequisites for the Petersen-Chapman method and collected representative length and weight data to ensure the reliability of estimates. According to Ricker (1975), the assumptions for reliable estimates with the Petersen-Chapman method are: (1) the marked and unmarked fish have the same natural mortality, (2) the marked and unmarked fish have same possibility of being caught, (3) there is no mark loss, (4) random mixing of marked fish to a population, (5) all marks are detected and reported, (6) there is only negligible recruitment to the catchable population during the recovery time. Assumptions 1–5 were fulfilled, since marking pike with T-bar anchor tags did not considerably increase the mortality in earlier studies and tag loss was negligible (Pierce and Tomcko 1993, Sharma and Borgstrøm 2008). Pike capture and recapture were conducted extensively on each lake to enable equal catchability for all pike. As pike handling, tagging and tag recording was conducted by trained personnel, mishandling, unreported tags, etc., unlikely affect the results. Fish passage from other lakes or rivers was restricted, because the study lakes are connected to other lakes only by small brooks which are either totally or at least partially impassable. Since lakes are reserved for research use only, no other fishing mortality than ours was expected to happen as there was only minimal evidence of illegal fishing. The major potential biases in our approach are related to the assumption concerning recruitment during recovery time. This was taken into account by including larger (≥ 35 cm) individuals in the analyses than had been earlier marked (≥ 30 cm) thereby excluding new recruits from the estimates. Possible error sources of the mark-recapture procedure and calculation with the Petersen method and comparison Bayesian estimates are more extensively discussed in the study of Kuparinen *et al.* (2012), which uses partially the same data from the years 2006–2009. Also regarding the catch-curve method, by which Z was estimated, the

key assumptions of this method were fulfilled: (1) there were no observed trends in recruitment during 2006–2008, (2) there was no fishing mortality during this period, (3) due to the multiple gears and sampling periods, there was relatively constant selectivity at age for the analysed ages ≥ 4 years. Older fully-recruited age group in Haukijärvi as compared with that in other lakes (9 years *vs.* 4 years) was not due to slower growth but lack of some smaller age groups in the data, which is likely explained by the small population size prone to high between-year variation (Lande 1993).

HSL in managing sustainable fisheries

Although HSL fishing proved to be better than MLL in maintaining population density, biomass and diverse size-structure, our results indicate that HSL fishing alone may not be sufficient to retain large individuals in a population, as we observed slightly decreasing numbers of large pike in both lakes with this type of fishing regulation. This implies that the fishing mortality of harvestable-sized pike in relation to growth rate was too high to let a sufficient amount of new recruits enter the largest size-class to maintain large pike over a longer period. Therefore, as suggested by Arlinghaus *et al.* (2010), fishing pressure has to be proportional to growth rate to ensure adequate recruitment of individuals exceeding the maximum length limit. Adjusting fishing pressure to a sustainable level may thus involve, beside HSL regulation, also other fisheries management tools such as bag limits, banning or restricting certain gear types, or restricting fishing areas or times (for example at spawning grounds or at spawning time) in order to control the fishing pressure on the pike population, as for example Paukert *et al.* (2001) and Pierce (2010) suggest.

Determining appropriate length limits for pike is an important task. The lakes we studied are small and have low production and slow pike growth (first author's unpubl. data). Therefore, the maximum length limit of 65 cm applied in this study is not likely to be valid everywhere. In their modelling study, Arlinghaus *et al.* (2010) suggested that ideal slot length limit for maintaining large pike is achieved by setting MLL of 45 cm and maximum length limit of 75–80 cm. In Sweden, in response to the declining pike stock in the coastal waters of the Baltic Sea, HSL is set to 40–75 cm with the daily bag limit of three pike. Recreational fishing is usually positively size-selective (Cook and Younk 1998, Lewin *et al.* 2006), and therefore implementing HSL regulation would be a promising tool to improve the sustainability of recreational fishing by maintaining high ecological status, and improving angling quality while still allowing a moderate mortality of medium-sized pike for subsistence fishing or low mortality by catch and release fishing.

Although implementing HSL regulation may decrease the maximum yield compared with that of MLL (Pierce *et al.* 1995), it can be considered an acceptable trade-off towards more sustainable fishing and diverse size distribution. Recreational fisheries in developed countries are often motivated by diverse leisure-related factors, e.g. the challenge of the catch, rather than simply maximizing biomass yield of the fishery (Arlinghaus 2006, Pierce 2010). Maintaining pike stock by HSL regulation requires catch-and-release practice for valuable large fish, which requires a certain skill level from the angler in order to minimize post-release mortality, injuries by hooking and handling and other sublethal alterations in physiology and behaviour (Cooke and Schramm 2007, Klefoth *et al.* 2008). According to our experience gained in this study as well as that of others (Tomcko 1997, Arlinghaus *et al.* 2008, Klefoth *et al.* 2008, Koski 2009, Ståhammar *et al.* 2014), pike is relatively resistant to catch and release fishing by angling with typically less than 5% mortality, which enables management of pike fisheries by HSL regulation. Furthermore, it has to be noted that our handling procedure, which included length and weight measurements, scale sampling, fin-clipping and tagging, was rougher than normal catch and release fishing.

Future challenges and conclusions

To ensure sustainable use of pike stocks in the long-term, it is important to increase our under-

standing of the ecological effects of pike fishing, and to manage pike fishing in a way which minimizes the harmful effect of fishing. Such knowledge will help preserving vital pike populations and their role in ecosystems, as well as socio-economic benefits of high-quality pike fisheries. Although the popularity of recreational fishing is expected to decrease in developed countries in the forthcoming years (FAO 2012), the pressure by recreational fishing on fish stocks may not decrease as there has been a rapid development in fishing techniques and fishing gear (Radonski 2002, Cooke and Cowx 2006). Managing pike fisheries in a sustainable manner is particularly important in the context of other human-induced impacts such as climate change, eutrophication and changes in hydro-morphological conditions, which may affect pike populations and increase their vulnerability to the negative effects of fishing (Allan *et al.* 2005, Lehtonen *et al.* 2009). To overcome the challenges pike stocks are increasingly facing today, while acknowledging the popularity of pike in recreational fishing and its high ecological importance and socio-economical value, it is imperative to develop sustainable fishing practices. In order to achieve this, fisheries stakeholders should be more active in implementing ambitious, even experimental methods to protect large pike, as also suggested by Carlson (2016).

To conclude, our study emphasizes the high potential of HSL regulation for conserving large fish, which is an essential feature in sustainable pike fishing. HSL proved to be better than MLL for maintaining a diverse population size and age structure. As per fisheries management, to maintain pike population vitality and natural ecosystem functioning, or to develop high-quality pike fishing (presence of trophy fish), regulation of pike fishing by HSL is advised. However, if fishing pressure on pike is considerable, also other fisheries regulation methods may be required.

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II

Harvestable slot-length limit maintains high production and consumption by northern pike (*Esox lucius*) in small forest lakes

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Abstract

In this eight-year experimental lake study, we compared the production and consumption responses in four northern pike (*Esox lucius*) populations to different size-selective fishing strategies: minimum length limit (MLL, 40 cm) and harvestable slot-length limit (HSL, 40- 64.9 cm) regulations. We also followed the effects of variable consumption by pike populations on the abundances of prey fish, European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The HSL enabled high pike production and consumption of roach and perch by diverse-sized pike. In one MLL-regulated lake, where the pike population collapsed, reduced consumption by pike allowed perch abundance to increase. In the other lakes, growth of pike increased as a compensatory response to high fishing mortality. As a result, pike production and prey fish consumption was maintained, and no changes in prey fish populations were observed.

Keywords

Northern pike, *Esox lucius*, production, consumption, bioenergetics, length limit regulation

1. Introduction

Northern pike, hereafter pike (*Esox lucius*) is a keystone species and apex predator in its circumpolar native distribution in the northern hemisphere thorough Europe, Asia and North America (Craig 1996). Pike has the potential to control abundance, size-structure and behavior of its prey species (Skov *et al*. 2002), as well as its own population through cannibalism (Raat 1988, Craig 1996). Due to its ubiquity, aggressiveness and large size, pike is one of the most targeted species in recreational

fishing in Europe and North America (Paukert *et al*. 2001, Arlinghaus *et al*. 2008). However, intensive harvesting of large predators may be detrimental, particularly in populations with low production, as removed biomass may exceed annual production (Pierce 2012, Rypel *et al*. 2015). As a result, the consumption by predatory fish may not be sufficient to control prey fish populations (Nilsson 2001), which can degrade and destabilize entire ecosystems (Kuparinen *et al*. 2016).

Fishing-induced reduction in biomass is often compensated by increased recruitment and growth of small and young fish (Walters and Martell 2004). Traditional fisheries management encourage to harvest large and old individuals to maximize the biomass yield, which is often implemented as use of minimum length limit regulation (henceforth MLL) (Paukert *et al*. 2001, Arlinghaus *et al*. 2010, Pierce 2010, Gwinn *et al*. 2015). Fishing-induced increase in growth and production is also reported for pike, which is due to decreased competition and cannibalism (Pierce and Tomcko 2003). However, prolonged fishing with MLL may reduce the overall production of pike populations due to biomass decline and evolutionary responses, i.e. stunted growth and decrease in maturation size and age, to heavily size-selective fishing, (Arlinghaus *et al*. 2010, Matsumura *et al*. 2011). These problems can be diminished by using harvestable slot length limit regulation (henceforth HSL) in which valuable large individuals are conserved (Oele *et al*. 2016, Tiainen *et al*. 2017). Although conservation of large individuals may initially produce lower biomass yields than MLL, in the long-term it may maintain production and harvestable biomass at a higher level than MLL, as the negative effects of MLL (size and age truncation, decrease of maturation size and age) are diminished (Arlinghaus *et al*. 2010, Matsumura *et al*. 2011, Gwinn *et al*. 2015, Vainikka *et al*. 2017). As lake-level experimental studies of length-limit –based management are rare, the assessment of productivity and prey fish consumption of this top predator species and popular gamefish has a high importance.

In this study we used growth analyses and bioenergetics modeling to assess how MLL of 40.0 cm and HSL of 40.0-64.9 cm affects the production of and consumption by pike populations, and how these were reflected in prey fish, European perch, hereafter perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) population abundances in four small, previously unfished forest lakes in Southern Finland. We tested three hypotheses:

1) Regardless of length limit regulations, the individual growth rate of pike will increase in all lakes due to lower competition for resources.

2) In MLL-lakes, the production and prey fish consumption of pike populations will decrease, because biomass is greatly reduced and size-distribution is truncated due to removal of large pike. In HSL-lakes, production and prey fish consumption of pike will remain more stable than in MLL-lakes despite fishing, because biomass and size-distribution of pike populations are less affected, and large individuals are maintained in the population.

3) In MLL-lakes, prey fish abundance will increase in response to decreased consumption by pike, whereas in HSL-lakes prey fish abundance will remain more stable.

2. Material and Methods

2.1. Study area

We examined pike growth, production and consumption in four small forest lakes, Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi (13.8, 2.1, 8.4 and 3.4 ha) in Evo region, southern Finland (61° 13' N; 25° 12' E) during years 2006–2013. These lakes have minimal anthropogenic impacts as no other activity than research is allowed, and agricultural and industrial pollution is negligible. The lakes are oligo-mesotrophic and naturally colored by humic substances with mean water color 130, 150, 330 and 340 mg Pt l^{-1} in Hokajärvi, Haarajärvi, Haukijärvi and Majajärvi, respectively (Olin *et al*. 2010). Secchi depths of the lakes are 1.5, 1.2, 0.8 and 0.65 m. and total phosphorus 7, 13, 11 and 29 µg l^{-1} in Hokajärvi, Haarajärvi, Haukijärvi and Majajärvi, respectively (Estlander *et al*. 2009). Vegetation coverage of study lakes is low, 4-15 %, except in Hokajärvi, where coverage is 80% (Tiainen *et al*. 2017). In all lakes, the dominating fish species are perch, roach and pike (Olin *et al*. 2010).

2.2. Fish population monitoring and size-selective fishing procedures

We conducted a capture-mark-recapture program in years 2006-2013 to determine pike population densities, biomasses and size structure distributions. We caught a total number of 830 pike of total length 30.0-100.5 cm during the study, of which 445 were from Haarajärvi, 49 from Haukijärvi, 222 from Hokajärvi and 114 from Majajärvi. We used multigear sampling (including fyke nets and wire traps at spawning time in late April-early-mid May and angling in late August-September) to avoid problems with gear selectivity and to improve catch and increase coverage. The mark-recapture procedure is described in more detail in Tiainen *et al.* (2017).

In years 2008-2012, we assessed two different experimental size-selective fishing strategies: MLL of 40.0 cm in Hokajärvi and Majajärvi, and HSL of 40.0-64.9 cm in Haarajärvi and Haukijärvi. Removal percentages (H_n) were 31.6 and 54.7 % of the estimated pike population ≥30 cm in 2008-2012 in HSL-lakes Haarajärvi and Haukijärvi and 39.6 and 60.4 % in MLL-lakes Hokajärvi and Majajärvi (Tiainen *et al*. 2017).

We also monitored perch population abundances in 2006-2013 by Schnabel multiple marking method (Seber 1982) in early spring. For perch monitoring, we used wire traps (12 x 12 mm mesh, 5 x 80 cm opening, Olin *et al*. 2016), and fin clipping as a group marking method (Horppila *et al*. 2010, Olin *et al*. 2016). We did not conduct mark-recapture for roach, due to their high mortality in handling. Instead, we

conducted a standard experimental gillnetting program (CEN 2005) annually three times in July-August. In gillnetting, we used Nordic multimesh gillnets (mesh size 5-55 mm) with stratified random sampling (Olin *et al*. 2016). Of gillnet catch, we derived biomass catch per unit effort (henceforth BPUE) of roach and perch as an index of their abundance.

2.3. Pike growth and dietary analysis

We determined age and back-calculated growth of pike from scales from released pike (n=521) or cleithrum-bones from killed pike (n=728) with a Fraser–Lee equation (Frost and Kipling 1959) or with a linear growth model (Casselman 1990) by 1-2 experienced readers. For the last year of the experiment, 2013, pike growth was not possible to directly determine by back-calculated growth analysis, due to incomplete annuli. We estimated growth in 2013 by fitting von Bertalanffy growth equation for each pike (n=70) individually. For those pike aforementioned methods were not applicable, we estimated growth either by yearly growth curve (n=52) (Casselman 1996) based on growth data from 2006-2012, or by linear growth equation based on individual growth history (n=26).

We analyzed a total number of 509 pike (TL=30.1-96.1 cm) stomachs (231 and 33 in HSL-lakes Haarajärvi and Haukijärvi and 165 and 80 in MLL-lakes Hokajärvi and Majajärvi) in 2006-2013. We excluded pike caught in spring by wire traps from dietary analysis, because we observed pike to feed on perch in wire traps. From pike stomachs, we sorted prey items taxonomically (fish, mammals and amphibians to species level, invertebrates to order level), counted, and determined the share of each prey item of the stomach volume by the points method (Hynes 1950, Windell, 1971, Hyslop 1980), at scale of 0-12 (0 = empty, 12 = full).

2.4. Bioenergetic modelling of pike production and consumption

Bioenergetics modeling can be used for investigating consumption rates of predators and evaluating impacts to prey populations (Stewart *et al*. 1981, Harfmart and Brandt 1995, Diana 1996). Modelling is based on the partition of ingested energy by the energetics equation C=G+R+F+U (Winberg 1956, Adams and Breck 1990), where C is the energy content of the food consumed, G is the energy used for growth (somatic and reproduction), R is the energy lost by respiration and F and U the energy losses to egestion and excretion, respectively. Respiration can be divided into three parts: the standard metabolic rate, specific dynamic action (SDA) and activity above standard metabolic rate. When growth, temperature, energy densities for the predator and prey and the specific parameter values for fish physiological processes are known, food consumption can be estimated (Adams and Breck 1990). When also population density, natural and fishing mortality are known, production and consumption can be calculated on population level (Hanson *et al*. 1997)

We used Fish Bioenergetics 3.0 (Hanson *et al*. 1997) to model pike production and consumption in study lakes. We calculated estimates for every lake, year and size-category, which were small=S (30.0-39.9 cm), medium=M (40.0-64.9 cm) and large=L (≥65 cm), and for sum of all of these, pike ≥30 cm, separately. We executed each bioenergetics run for initial population size of 100 individuals. Production and consumption estimates obtained were corrected in relation to size-category-specific density estimates (Tiainen *et al*. 2017). As density estimates were available only for ≥35 cm pike, we used the relative abundance of 30.0-34.9 cm pike in length frequency distribution as proxy of abundance of 30.0-34.9 cm pike in the population.

We derived weight increment during growing season for each size category from size-structure distributions, back-calculated growth data, and lake-specific length-mass power regression equations: m = 0.005 $L^{3.0183}$ (r^2 = 0.9792) in Haarajärvi, m = 0.0037 $L^{3.1168}$ (r^2 = 0.991) in Haukijärvi, m = 0.0037 $L^{3.1127}$ (r^2 = 0.9837) in Hokajärvi and m = 0.0043 $L^{3.0862}$ (r^2 = 0.9915) in Majajärvi, in which m = estimated mass (g), L total length (mm) and r^2 = coefficient of determination.

We calculated production and consumption estimates for pike for growing season (1st of May-12th of October, water temperature roughly ≥ 6° C) instead of year, as we assumed pike feeding, and consequently growth, production and consumption to take place within this period. Also, unrealistic negative production estimates were produced by the bioenergetic model in water temperatures near zero. The applicability of the default pike physiological parameters provided by Fish Bioenergetics 3.0 to northern latitudes has earlier been criticized by Jacobson (1992) and Heikinheimo and Korhonen (1996). We considered default optimum temperature for pike of the model (24°C) too high, and instead we used more relevant values: optimum temperature for growth of 21 °C for small and medium-sized pike and of 19 °C for large pike (Pierce *et al*. 2013), and maximum temperature of 29.4 °C (Casselman 1978). Otherwise we used default parameters of program for pike (Hanson *et al.* 1997) in the model.

We collected temperature data (see Appendix) from study lakes by HOBO temperature loggers in 2006-2011 and Alpha Mach iBCod G_1 -loggers in 2012-2013 from 1 m depth at the interval of 4 hrs. We set spawning day as 10th of May with 10 % weight loss for both sexes (Frost and Kipling 1967, Lappalainen *et al*. 2013) for size-classes M and L and 5 % for size-class S, as roughly a half of all pike at that length were not mature. We derived the yearly fishing mortality (percentage of standing biomass) from removal catch data of each size-class, and divided mortality to occur at three periods: spring (fyke-netting and wire-trapping from 1st-20th of May, summer (gillnetting in 19th-29th of July) and autumn (angling from 28th of August - 7th of October). In MLL-lakes Hokajärvi and Majajärvi in 2011, when largest size-class were extinct by pike removal, we set their mortality to 100 % at corresponding time of capture (spring or autumn) and used observed growth past the last annuli to calculate production and consumption estimates. We estimated annual natural mortality N by equation $N = 1\text{-}e^{-z}$, in which $-z$ is the instantaneous mortality rate, calculated by the catch-curve method

(Robson and Chapman 1961) and derived from Tiainen *et al*. (2017). We expected the constant values of *N* during modelled growing season: 0.21 in Haarajärvi, 0.19 in Haukijärvi, 0.24 in Hokajärvi and 0.27 in Majajärvi.

For bioenergetic analysis, we divided prey items into 3 subcategories according to stomach fullness analysis for each lake separately; fish (all species combined), invertebrates and other (amphibians and mammals combined). For all fish species, we used energy content of yellow perch (*Perca flavescens*), 4186 Kj g^{-1}, which value (or very close by) is used in many bioenergetic studies (Carline 1987, Heikinheimo and Korhonen 1996, Keskinen *et al*. 2008). For invertebrates, we used energy content of 3348 Kj g^{-1} (Salonen *et al.* 1976) and for other prey items (amphibians and mammals), we used energy content of 4210 Kj g^{-1}, which represents an average of energy contents of mammals and amphibians as calculated by Kloskowski (1999). As the proportional usage of invertebrates, roach and perch did not differ within-lake between size-categories, and use of other prey items were marginal, we used the same proportions of the three prey subcategories for all sizes of pike. As pike consumption consisted mainly on fish, (average percentage 95.5, 95.3, 88.7 and 98.2 % in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi respectively), the majority of which (75.6 - 94.9 %) were roach and perch, we calculated prey species-specific consumptions estimates for those species only.

From bioenergetic analyses, we calculated three outputs: production of pike biomass (kg ha^{-1}), prey fish consumption by biomass, and production/consumption ratio (hereafter P/C), which indicates energy allocated for growth during the study period (Hanson *et al*. 1997, Christensen *et al*. 2009, Lin *et al*. 2012). We calculated all the output variables for years 2006-2013 and for size-classes S, M and L, and for total population (pike ≥30 cm). Corresponding abbreviations for total population, and for S, M and L-sized pike for production are P_{tot}, P_S, P_M and P_L, for consumption C_{tot}, C_S, C_M and C_L and P/C_{tot}, P/C_S, P/C_M and P/C_L for P/C. In Haarajärvi, year 2006 was excluded from the analysis due to unrepresentative high an inaccurate population estimate (Tiainen *et al*. 2017), which produced biased production and consumption estimates.

2.5. Statistical analysis

To determine the growth-responses to MLL and HSL, we analysed the between-year differences (2008 vs. 2012; i.e. first year vs. last year of pike removal) in pike length at age (from 2 to 12 yr.) by lake-specific repeated ANOVA with Wald statistics and Bonferroni corrections in pairwise comparisons. The analysis included two fixed variables (year and individual), and back-calculated age was the repeated factor with compound symmetry as covariance structure (Horppila and Nyberg 1999).

To examine the yearly trends in pike production, consumption and P/C as response to HSL and MLL, fitted general linear model with repeated measures by SAS version 9.4 for each lake separately for total population and size-classes S, M and L. In these analyses, we used data from years 2008-2013, as 2008 represents a baseline value

referring to the level of production and consumption before the pike removal experiment, and 2013 represents the final year of the experiment.

We analyzed the effects of pike consumption on the estimated perch biomass and on the gillnet BPUEs of perch and roach by linear regression analysis for each lake separately by IBM SPSS Statistics 23. We conducted tests for roach or perch gillnet BPUE, or perch biomass estimate as a dependent variable, and pike consumption on roach or perch as independent variable. We used ln (x+1) transformed data in all statistical calculations.

When analyzing the effect of pike consumption on perch and roach BPUEs, we used consumption estimates and BPUE's from equivalent years, as gillnetting was conducted within the same growing season as pike consumption took place, in mid and late summer in July-August. In the analysis of pike consumption and perch biomass estimate, we used the consumption estimates as a predictor of perch density estimate at spring of the following year. In the case of Lake Haarajärvi, we excluded year 2006 as an outlier from the analysis, see above.

3. Results

3.1 Pike growth

Pike growth in study lakes was low, and six-year old pike were on average 39.2, 40.5, 37.0 and 39.1 cm (total length) in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Fig. 1). Pike growth increased in both HSL-lakes, as indicated by statistically significant increase in length-at-age in age groups 2-10 yrs. in Haarajärvi and age groups 3 and 6 yrs. in Haukijärvi from 2008 to 2013 (Fig. 1, Table 1). Of MLL-lakes, pike length-at-ages of 2, 4, 5 and 10 yrs. old pike increased in Hokajärvi, but in Majajärvi the only growth response was the decrease in mean length of 12 yrs. old pike (p=0.010) (Fig. 1, Table 1).

3.2 Production and consumption

The average total production (P_{tot}) of the ≥30 cm pike population in 2006-2013 was 2.4 (SD 0.72) and 2.1 (SD 0.88) kg ha^{-1} yr^{-1} in HSL-lakes Haarajärvi and Haukijärvi, and 1.9 (SD 0.51) and 2.3 (SD 1.36) kg ha^{-1} yr^{-1} in MLL-lakes Hokajärvi and Majajärvi. Large pike represented on average 17.5, 38.4, 8.5 and 10.2 % share of the total production in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Fig. 2). In HSL-lakes, none of P_{tot}, P_S, P_M or P_L expressed a statistically significant trend ($p > 0.05$) during the study period (Fig. 2, Table 2). In MLL-lake Hokajärvi, P_S expressed an increasing trend (p=0.027) from 2008 to 2013. In the other MLL-lake, Majajärvi, pike production decreased from level of 3.7 (2006-2008 average) to <1 kg ha^{-1} in 2013. As a result, P_{tot}, (p=0.006), P_S (p=0.004), P_M (p=0.038) and P_L (p=0.031) showed significant decreasing trends (Fig. 2, Table 2).

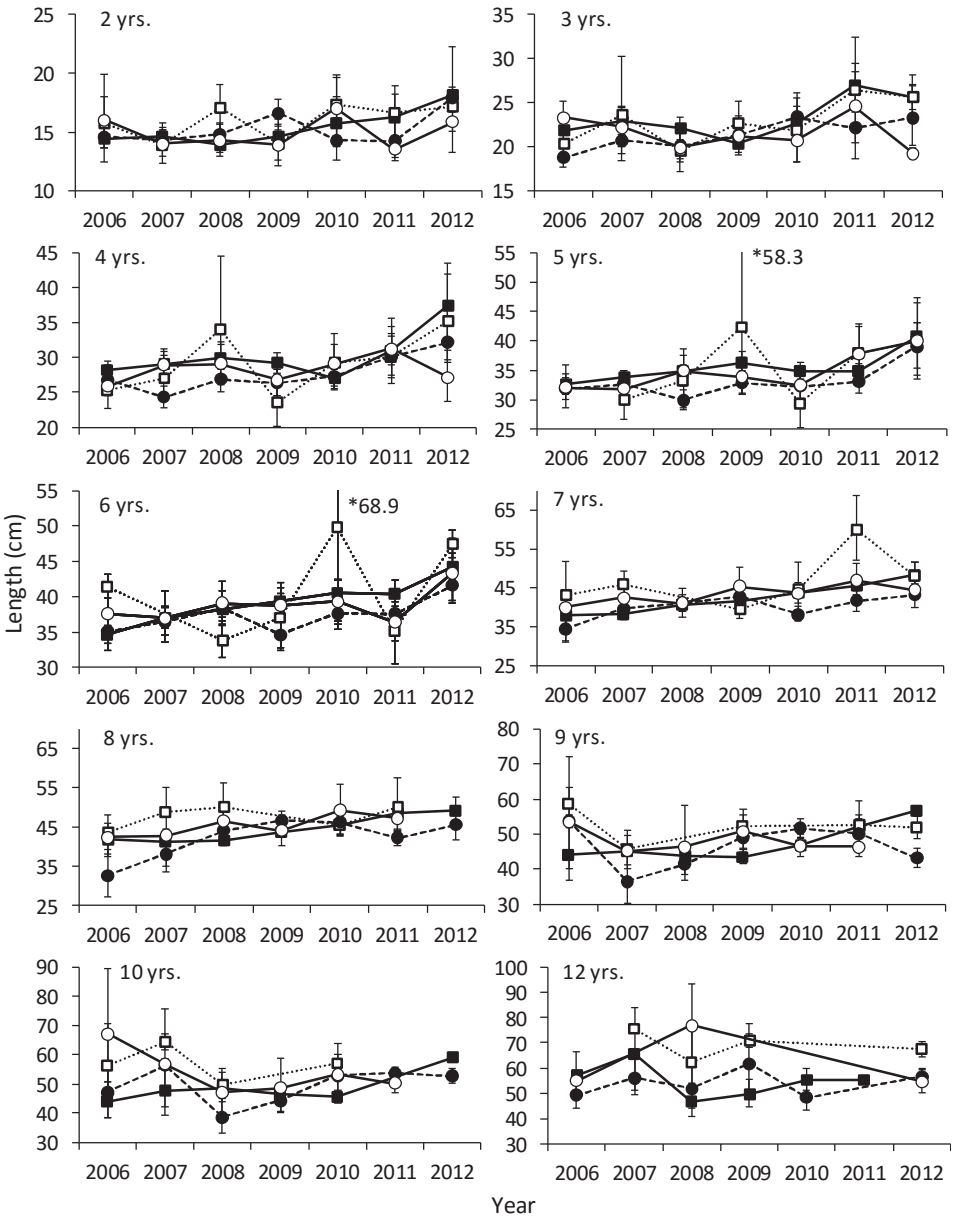

Figure 1. Average lengths and SDs of pike age groups 2-10 and 12 yrs. in study lakes in 2006-2012. Closed square = Haarajärvi (HSL), open square = Haukijärvi (HSL), closed circle = Hokajärvi (MLL) and open circle = Majajärvi (MLL). HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation. Note different scales of y-axis.

Table 1. Pairwise-comparisons (adjusted Bonferroni) of repeated ANOVA for mean lengths of age groups containing sufficient number of individuals for testing in 2008 and 2012. HSL=Harvestable slot length limit regulation, MLL=Minimum length limit regulation. Significant values are in bold.

Lake	Age	Estimate	S.E.	*z*-value	*p*-value
Haarajärvi	2	-0.268	0.02897	-9.25	**<0.001**
HSL	3	-0.1492	0.05437	-2.74	**0.012**
	4	-0.2208	0.08209	-2.69	**0.007**
	5	-0.1556	0.03382	-4.6	**<0.001**
	6	-0.1466	0.02697	-5.44	**<0.001**
	7	-0.167	0.03836	-4.36	**<0.001**
	8	-0.1695	0.03782	-4.48	**<0.001**
	9	-0.261	0.02135	-12.23	**<0.001**
	10	-0.1968	0.05364	-3.67	**<0.001**
Haukijärvi	2	-0.00824	0.1433	-0.06	0.954
HSL	3	-0.2672	0.07024	-3.8	**<0.001**
	4	-0.03425	0.1608	-0.21	0.972
	5	-0.1826	0.1095	-1.67	0.330
	6	-0.3359	0.04419	-7.6	**<0.001**
	12	-0.07648	0.1148	-0.67	0.879
Hokajärvi	2	-0.1922	0.02902	-6.63	**<0.001**
MLL	3	-0.1474	0.08184	-1.8	0.311
	4	-0.1798	0.05799	-3.1	**0.013**
	5	-0.265	0.05793	-4.58	**0.001**
	6	-0.08365	0.04373	-1.91	0.291
	7	-0.05057	0.04731	-1.07	0.739
	8	-0.03563	0.0555	-0.64	0.521
	9	-0.03668	0.05102	-0.72	0.721
	10	-0.3112	0.08278	-3.76	**0.002**
	12	-0.08504	0.08795	-0.97	0.704
Majajärvi	2	-0.1067	0.0561	-1.9	0.298
MLL	3	0.0334	0.04639	0.72	0.472
	4	0.06858	0.08647	0.79	0.672
	5	-0.1345	0.09561	-1.41	0.406
	6	-0.1055	0.06569	-1.61	0.367
	7	-0.07991	0.04951	-1.61	0.431
	12	0.3394	0.1065	3.19	**0.010**

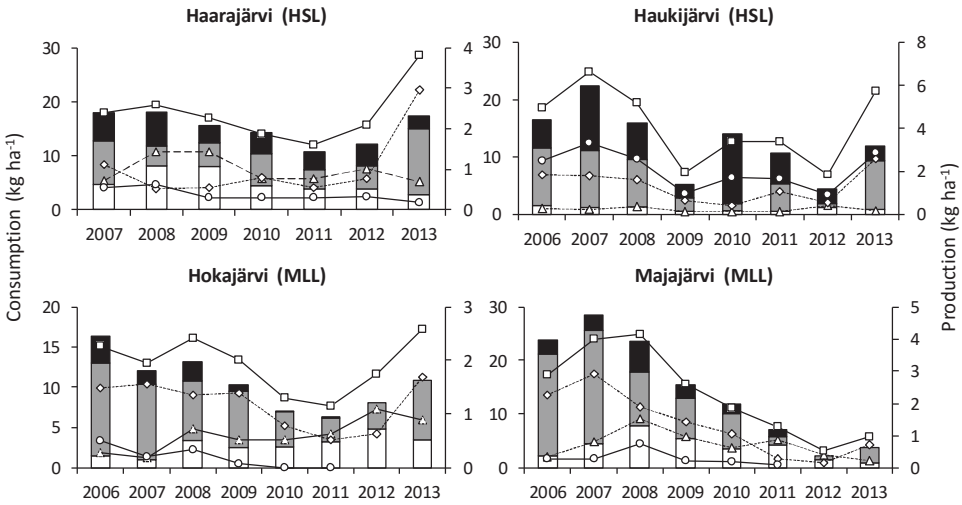

Figure 2. Development of pike production and consumption (kg ha^{-1}) of prey fish by 30.0-39.9 cm (triangle and white bar), 40.0-64.9 cm (tilted square and grey bar) and ≥65 cm pike (circle and black bar), and by total pike population (square and total bar height) in 2006-2013, except in Haarajärvi in 2007-2013. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation. Note different scales of both y-axis.

The total consumption of pike on prey fish was on average 18.4 (SD 9.3) and 12.6 (SD 5.9) kg ha^{-1} in HSL-lakes Haarajärvi and Haukijärvi and 10.5 (SD 3.41) and 14.6 (SD 9.9) kg ha^{-1} in MLL-lakes Hokajärvi and Majajärvi. Consumption by large pike represented on average 27.3, 47.6, 9.8 and 15.8 % of the total consumption in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Fig. 2). In HSL-lakes no clear trend was detected in C_{tot} (p>0.05, Table 3), although consumption first decreased from 18.1 (2008) to 10.8 kg ha^{-1} (2011) in Haarajärvi and from 15.9 (2008) to 4.6 kg ha^{-1} (2012) in Haukijärvi, but recovered until 2013 in both lakes (Fig. 2). C_S expressed a decreasing trend in Haarajärvi (p = 0.010), but in Haukijärvi no trends were detected in consumption of any size class (Fig. 2, Table 3). In MLL-lake Hokajärvi, total consumption did not express any trend (p>0.05), but C_S increased almost significantly (p=0.050). C_L decreased as a result of extinction of large pike although this trend was not statistically significant during the period when large pike were observed (Fig. 2, Table 3). In Majajärvi, the total consumption by the pike population during the study period was initially the highest of the study lakes, 25.3 kg ha^{-1} (2006-2008 average), but it decreased to <4 kg ha^{-1} until 2013 (p=0.004). A similar decreasing trend was observed also in C_S (p=0.016), C_M (p=0.030) and C_L (p<0.001) as a result of pike population collapse (Fig. 2, Table 3).

Table 2. Trends in pike production by total population (P_{tot}), 30.0-39.9 cm (P_S), 40.0-64.9 cm (P_M) and ≥65 cm (P_L) pike in 2006-2013 analyzed by a general linear model with repeated measures. Significant values are in bold. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake		Effect	Estimate	S.E.	DF	*t*-value	*p*-value
Haarajärvi	P_{tot}	Intercept	2437.98	947.45	0	2.57	.
HSL		y2	24.2398	243.28	4	0.1	0.925
	P_L	Intercept	707.22	171.49	0	4.12	.
		y2	-94.4016	44.0343	4	-2.14	0.099
	P_M	Intercept	336.57	844.72	0	0.4	.
		y2	235.98	216.91	4	1.09	0.338
	P_S	Intercept	1394.19	213.55	0	6.53	.
		y2	-117.34	54.8343	4	-2.14	0.099
Haukijärvi	P_{tot}	Intercept	1791.08	883.55	0	2.03	.
HSL		y2	8.5457	226.87	4	0.04	0.972
	P_L	Intercept	1075.69	365.44	0	2.94	.
		y2	-118.64	93.8363	4	-1.26	0.275
	P_M	Intercept	533.14	852.29	0	0.63	.
		y2	118.21	218.85	4	0.54	0.618
	P_S	Intercept	182.25	111.57	0	1.63	.
		y2	8.9815	28.6474	4	0.31	0.770
Hokajärvi	P_{tot}	Intercept	1745.19	570.2	0	3.06	.
MLL		y2	25.3836	146.41	4	0.17	0.871
	P_L	Intercept	270.63	95.3887	0	2.84	.
		y2	-56.8636	24.4936	4	-2.32	0.081
	P_M	Intercept	1229.21	512.22	0	2.4	.
		y2	-41.4811	131.53	4	-0.32	0.768
	P_S	Intercept	245.35	140.44	0	1.75	.
		y2	123.73	36.061	4	3.43	**0.027**
Majajärvi	P_{tot}	Intercept	3858.38	419.11	0	9.21	.
MLL		y2	-582.98	107.62	4	-5.42	**0.006**
	P_L	Intercept	1131.49	162.07	0	6.98	.
		y2	-135.51	41.6148	4	-3.26	**0.031**
	P_M	Intercept	2275.98	464.03	0	4.9	.
		y2	-363.49	119.15	4	-3.05	**0.038**
	P_S	Intercept	450.91	55.5436	0	8.12	.
		y2	-83.9819	14.2623	4	-5.89	**0.004**

Table 3. Trends in pike consumption by total population (C_{tot}), 30.0-39.9 cm (C_S), 40.0-64.9 cm (C_M) and ≥65 cm (C_L) pike in 2006-2013 analyzed by general linear model with repeated measures. Significant values are in bold. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake		Effect	Estimate	S.E.	DF	*t*-value	*p*-value
Haarajärvi	C_{tot}	Intercept	21411	4523.55	0	4.73	.
HSL		y2	-1556.9	1161.54	4	-1.34	0.251
	C_L	Intercept	6577.9	1415.24	0	4.65	.
		y2	-705.76	363.4	4	-1.94	0.124
	C_M	Intercept	5787.32	3631.5	0	1.59	.
		y2	261.52	932.48	4	0.28	0.793
	C_S	Intercept	9045.67	927.96	0	9.75	.
		y2	-1112.66	238.28	4	-4.67	**0.010**
Haukijärvi	C_{tot}	Intercept	14452	5041.4	0	2.87	.
HSL		y2	-1050.11	1294.51	4	-0.81	0.463
	C_L	Intercept	8438.91	3698.99	0	2.28	.
		y2	-858.83	949.81	4	-0.9	0.417
	C_M	Intercept	5033.42	3893.22	0	1.29	.
		y2	-160.57	999.69	4	-0.16	0.880
	C_S	Intercept	979.39	360.59	0	2.72	.
		y2	-30.7119	92.5905	4	-0.33	0.757
Hokajärvi	C_{tot}	Intercept	11591	2705.13	0	4.28	.
MLL		y2	-634.5	694.61	4	-0.91	0.413
	C_L	Intercept	1938.18	643.53	0	3.01	.
		y2	-405.01	165.24	4	-2.45	0.070
	C_M	Intercept	8064.77	2427.65	0	3.32	.
		y2	-662.95	623.36	4	-1.06	0.348
	C_S	Intercept	1587.89	608.2	0	2.61	.
		y2	433.46	156.17	4	2.78	**0.050**
Majajärvi	C_{tot}	Intercept	26170	2884.69	0	9.07	.
MLL		y2	-4334.68	740.72	4	-5.85	**0.004**
	C_L	Intercept	4212.49	307.39	0	13.7	.
		y2	-758.15	78.9303	4	-9.61	**<0.001**
	C_M	Intercept	15428	3191.63	0	4.83	.
		y2	-2690.23	819.54	4	-3.28	**0.030**
	C_S	Intercept	6529.07	858.41	0	7.61	.
		y2	-886.31	220.42	4	-4.02	**0.016**

The average P/C ratio of the pike population in 2006-2013 was 0.153 (SD=0.030), 0.171 (SD=0.038), 0.188 (SD=0.030) and 0.178 (SD=0.044) in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively (Table 4). In HSL-lake Haarajärvi P/C_{tot} showed an increasing trend (p=0.045) from 0.137 in 2008 to 0.221 in 2013 (62% relative increase). P/C_S and P/C_M also showed increasing trends during this interval (p=0.009 and 0.029), but in contrast, P/C_L showed a decreasing trend (p=0.046) (Fig. 3, Table 4). In the other HSL-lake, Haukijärvi, significant trends were not detected (p>0.05), although the increase in P/C_{tot} from 2008 to 2013 was almost equal to Haarajärvi, (64% relative increase, Fig. 3, Table 4).

Table 4. Trends in pike production/consumption ratio by total population (P/C_{tot}), 30.0-39.9 cm (P/C_S), 40.0-64.9 cm (P/C_M) and ≥65 cm (P/C_L) pike in 2006-2013 analyzed by general linear model with repeated measures. Significant values are in bold. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake		Effect	Estimate	S.E.	DF	*t*-value	*p*-value
Haarajärvi	P/C_{tot}	Intercept	0.1031	0.01876	0	5.49	.
HSL		y2	0.01388	0.004817	4	2.88	**0.045**
	P/C_L	Intercept	0.1002	0.006529	0	15.35	.
		y2	-0.00479	0.001677	4	-2.86	**0.046**
	P/C_M	Intercept	0.0885	0.0223	0	3.97	.
		y2	0.01901	0.005727	4	3.32	**0.029**
	P/C_S	Intercept	0.1262	0.01583	0	7.97	.
		y2	0.0192	0.004064	4	4.72	**<0.001**
Haukijärvi	P/C_{tot}	Intercept	0.1181	0.03145	0	3.76	.
HSL		y2	0.01442	0.008076	4	1.79	0.149
	P/C_L	Intercept	0.1299	0.01463	0	8.88	.
		y2	-0.0025	0.003755	4	-0.67	0.542
	P/C_M	Intercept	0.1485	0.02421	0	6.13	.
		y2	0.01642	0.006217	4	2.64	0.058
	P/C_S	Intercept	0.1846	0.03767	0	4.9	.
		y2	0.01281	0.009672	4	1.32	0.256
Hokajärvi	P/C_{tot}	Intercept	0.1361	0.01146	0	11.87	.
MLL		y2	0.01111	0.002944	4	3.77	**0.020**
	P/C_L	Intercept	0.138	0.02957	0	4.67	.
		y2	-0.02759	0.007593	4	-3.63	**0.022**
	P/C_M	Intercept	0.1387	0.01389	0	9.98	.
		y2	0.008537	0.003568	4	2.39	0.075
	P/C_S	Intercept	0.1596	0.0155	0	10.3	.
		y2	0.008743	0.003981	4	2.2	0.093
Majajärvi	P/C_{tot}	Intercept	0.1127	0.01671	0	6.74	.
MLL		y2	0.02066	0.004292	4	4.81	**0.009**
	P/C_L	Intercept	0.146	0.02097	0	6.96	.
		y2	-0.02407	0.005385	4	-4.47	**0.011**
	P/C_M	Intercept	0.1345	0.022	0	6.11	.
		y2	0.01439	0.005648	4	2.55	0.063
	P/C_S	Intercept	0.1361	0.01938	0	7.02	.
		y2	0.01918	0.004976	4	3.85	**0.018**

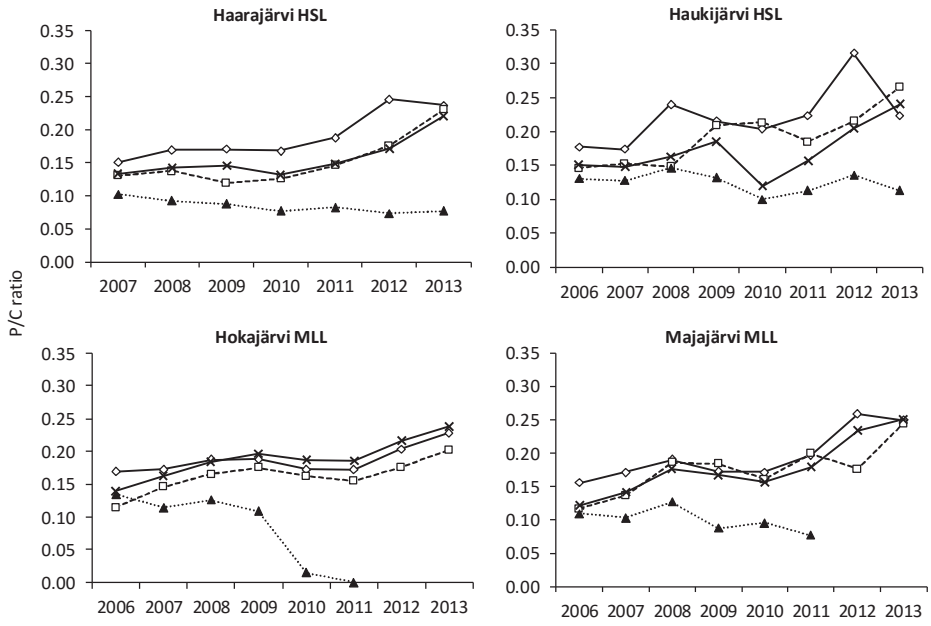

Figure 3. Development of pike production/consumption ratio of 30.0-39.9 cm (tilted square), 40.0-64.9 cm (square) and ≥65 cm pike (triangle), and total pike population (cross) in 2006-2013, except in Haarajärvi in years 2007-2013. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

In MLL-lakes Hokajärvi and Majajärvi, P/C_{tot} showed a 68.2 % and 58.4 % statistically significant increase (p=0.020 and 0.009), from 0.162 to 0.237 and from 0.146 to 0.239, respectively (Fig. 3, Table 4). However, the increases in P/C_S and P/C_M in Hokajärvi were not statistically significant, and P/C_L showed a decreasing response during the period when large pike were observed (2006- 2011) (Fig. 3, Table 4). In Majajärvi P/C_S showed a statistically significant increase (p=0.018), but P/C_M did not, and P/C_L decreased (p=0.011) (Table 4).

3.3 Effects on prey fish populations

Pike population consumed on average 60.4, 49.9, 42.9 and 31.8 % of estimated perch spring biomass in Haarajärvi, Haukijärvi, Hokajärvi and Majajärvi, respectively, in 2006-2013 (Fig. 4). In regression analysis we found there was statistically significant negative relationship in Majajärvi between pike consumption on perch and perch gillnet BPUE (p = 0.038), but not between consumption on roach and roach gillnet BPUE (p > 0.05) (Figs. 4 and 5, Table 5). In other lakes no statistically significant relationship (p > 0.05) was found between pike consumption and perch density estimates or on perch or roach gillnet BPUEs (Figs 4 and 5, Table 5).

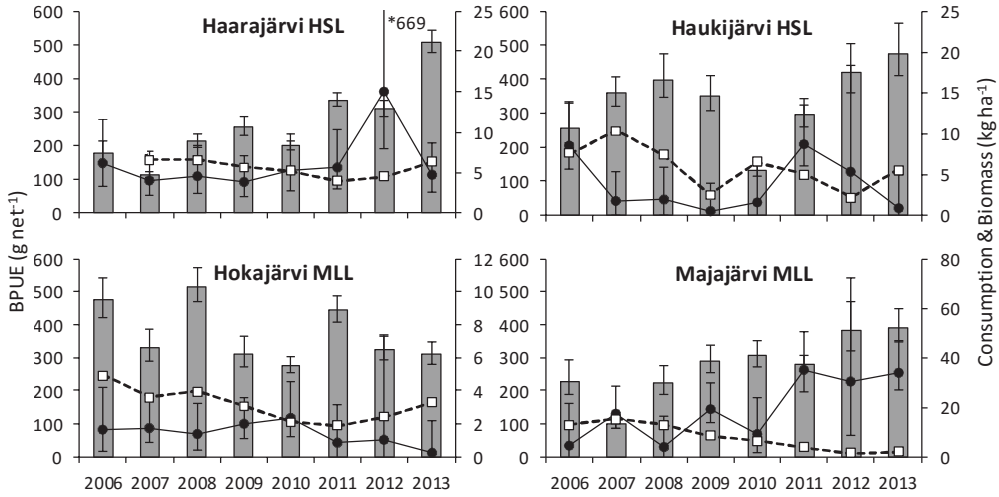

Figure 4. Pike consumption of perch by biomass (open square) and perch biomass estimates (grey bar, right y-axis) and perch BPUEs (dot, left y-axis) in the study lakes in 2006-2013. For Haarajärvi consumption estimate for 2006 is not presented. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation. Note different scales of y-axis.

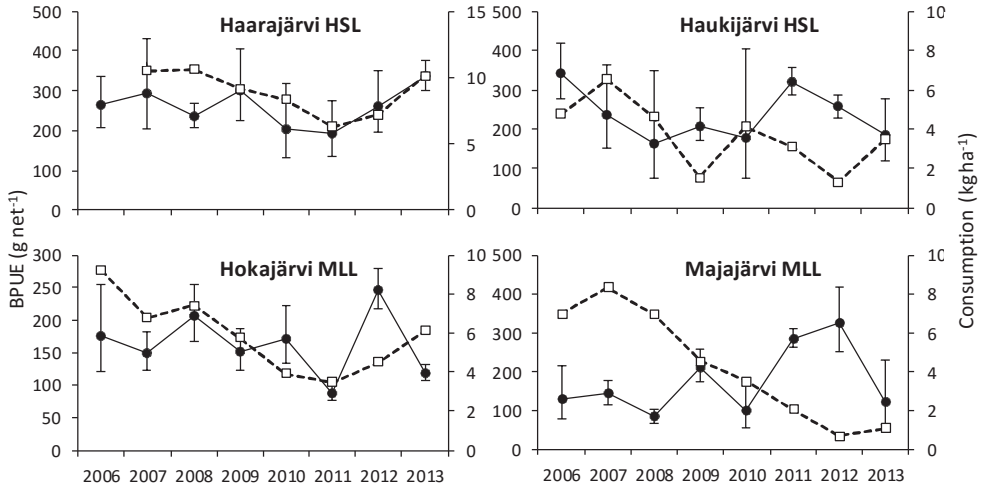

Figure 5. Pike consumption of roach by biomass (open square, right y-axis) and roach BPUEs (dot, left y-axis) in study lakes in 2006-2013. For Haarajärvi consumption estimate for 2006 is not presented. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation. Note different scales of y-axis.

Table 5. Responses of perch biomass estimates and perch and roach gillnet BPUE's on pike consumption in study lakes in 2006-2013 analyzed by linear regression. Significant values are in bold. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.

Lake	Test	Effect	Estimate	S.E.	*t*-value	*p*-value
Haarajärvi	Consumption vs.	Constant	4.79	1.27	3.772	0.020
HSL	perch biomass	c_perch	-1.21	0.69	-1.757	0.154
	Consumption vs.	Constant	5.31	0.99	5.386	0.002
	perch BPUE	c_perch	-0.21	0.49	-0.423	0.687
	Consumption vs.	Constant	5.86	0.48	12.105	<0.001
	roach BPUE	c_roach	0.13	0.2	0.622	0.557
Haukijärvi	Consumption vs.	Constant	2.21	0.63	3.511	0.017
HSL	perch biomass	c_perch	0.26	0.33	0.778	0.472
	Consumption vs.	Constant	3.61	1.76	2.045	0.087
	perch BPUE	c_perch	0.23	0.93	0.251	0.810
	Consumption vs.	Constant	6.14	0.41	15.065	<0.001
	roach BPUE	c_roach	-0.04	0.27	-0.153	0.883
Hokajärvi	Consumption vs.	Constant	2.12	0.47	4.513	0.006
MLL	perch biomass	c_perch	-0.03	0.33	-0.084	0.936
	Consumption vs.	Constant	3.8	1.62	2.35	0.057
	perch BPUE	c_perch	0.22	1.14	0.19	0.855
	Consumption vs.	(Constant)	4.91	0.87	5.623	0.001
	roach BPUE	c_roach	0.42	0.46	0.915	0.396
Majajärvi	Consumption vs.	Constant	4.44	0.48	9.317	<0.001
MLL	perch biomass	c_perch	-0.41	0.22	-1.893	0.117
	Consumption vs.	Constant	6.41	0.68	9.409	<0.001
	perch BPUE	c_perch	-0.86	0.33	-2.647	**0.038**
	Consumption vs.	Constant	6.37	0.42	15.024	<0.001
	roach BPUE	c_roach	-0.44	0.26	-1.67	0.146

4. Discussion

4.1. Responses of pike growth to HSL and MLL

As we hypothesized, pike growth increased (at least in some age-groups) in other study lakes than Majajärvi as a response to removal fishing by HSL or MLL. The growth response was the clearest in the two largest study lakes Haarajärvi (HSL) and Hokajärvi (MLL), probably due to larger sample size compared to smaller lakes. In general pike growth was slow in all study lakes, but comparable to the study of Raitaniemi (1995) in small humic lakes, in which pike reached a length of 35 on average cm at age 4 yrs. Also, Margenau *et al*. (1998) have reported stunted growth of pike in small Northern Wisconsin lakes after total length of 53 cm due to variety of environmental and density-related factors. Unfavorable environmental conditions likely explain slow growth in this study as well, as the lakes are oligo-mesotrophic and have strong temperature stratification and consequently hypoxic hypolimnion during summer and winter, restricting fish to a thin oxygenated layer (Rask *et al*. 1999). The only exception to this in our study is Haarajärvi, where the hypolimnion is well oxygenated throughout the year (Olin *et al*. 2010). This may have contributed to the fact that Haarajärvi showed the clearest growth response of all study lakes, as length-of-age of 2-10 yrs. old pike increased. A deep oxygenated layer is crucial for growth of large pike, as they favor deeper and cooler water than their smaller conspecifics (Diana 1996, Pierce *et al*. 2013).

In general the study lakes have also low euphotic depth and steep banks, and littoral vegetation is narrow (coverage 4-15 %), resulting in limited habitats for pike and its prey species. The only exception is Hokajärvi, where littoral vegetation coverage is 80 % (Tiainen *et al*. 2017). However, Hokajärvi is the most oligotrophic (indicated by the lowest total phosphorus values and highest water transparency) of the study lakes, and also displays the lowest perch population density (Olin *et al*. 2016), indicating that in Hokajärvi growth of pike may be limited by food resources. Widespread vegetation cover and high water transparency affects positively on pike growth (Casselman 1996), which may explain the strong growth response of small pike due to released resources by pike removal.

On the contrary to Hokajärvi, Majajärvi has the highest total phosphorus (TP) concentration of all study lakes and highest perch density (Olin *et al*. 2016), but challenging environmental conditions including a narrow euphotic zone, low transparency, and narrow oxygenated layer. These restricting factors have possibly contributed to the observed slow growth and also hindered the positive growth response to increased resources per capita. Such conditions may also increase the vulnerability of pike to MLL-type fishing, as fast growing phenotypes are removed by fishing, and remaining slowly-growing and early maturing individuals are unable to utilize released resources on growth (Diana 1983, Kokkonen *et al*. 2015). MLL may

thus affect negatively the growth in long-term due to evolutionary responses induced by positively size-selective fishing (Arlinghaus *et al*. 2010, Matsumura *et al*. 2011).

4.2. Responses of pike production to HSL and MLL

Estimated pike production values in the study lakes were comparable to an earlier study (Rask and Arvola 1985) in the same area (1.9-2.4 vs. 2.6 kg ha^{-1} yr^{-1}), but lower than in the study of Pierce and Tomcko (2003) in seven Minnesota lakes, where production averaged 4.1 (range 0.8-8.3) kg ha^{-1} yr^{-1}. In HSL-lakes Haarajärvi and Haukijärvi, pike production first decreased but recovered to the initial level by the end of the study period despite intensive fishing. Pike removal was not conducted in 2013, which is a likely reason for production recovery in 2013. In our earlier study (Tiainen *et al*. 2017), HSL maintained higher population density and biomass and more diverse size-structure compared to MLL. Although there were indications of a slight decrease in population density in both lakes, this was largely compensated by increased growth, as growth of individual pike is negatively density-dependent (Pierce and Tomcko 2003). Positive response in growth was also manifested in increased recruitment into medium size range in Haarajärvi, as biomass of M-sized pike was greatest in 2013 (Tiainen *et al*. 2017). This result indicates the potential of pike populations to compensate mortality by fishing under HSL. According to our study, HSL can maintain pike production provided that the growth rate is enhanced.

Pike production in two MLL-lakes reacted differently to pike removal. In Hokajärvi, production recovered after an initial decrease, due to increased production of small pike. Both density (Tiainen *et al*. 2017) and growth of small and young (2, 4 and 5 yrs.) pike increased, which compensated the fishing mortality, as we hypothesized. In MLL-lake Majajärvi, pike production decreased considerably, as there were no signs of increased growth in any age group or recruitment to compensate the decrease in population density due to removal fishing. The observed decrease in pike production in Majajärvi supports the recent criticism of MLL by Arlinghaus *et al*. (2010), Pierce (2010) and Gwinn *et al*. (2015), according to whom low MLL and high exploitation rate may lead to decrease in yield.

4.3. Responses of pike consumption and P/C on fishing by HSL and MLL

Pike consumption in HSL-lakes followed the same pattern which was observed in production: an initial decrease followed by a recovery. All size classes contributed to the total consumption, suggesting that pike populations have the potential to consume diverse-sized prey, thus affecting the food web structure more efficiently (Nilsson 2001). In Haarajärvi the only clear response to HSL was the decrease of consumption by small pike (30.0-39.9 cm), which is interesting, as pike of this size were not targeted by fishing. The results may indicate natural variability in age class strength, since density of small pike reached its minimum in Haarajärvi in 2013 (Tiainen *et al*. 2017), or alternatively a decreased timespan in size-class 30.0-39.9 cm due to increased

growth. In the other HSL-lake, Haukijärvi, production by small, medium and large pike fluctuated, reflecting variation in population estimates due to small sample size (Tiainen *et al.* 2017) or environmental and demographic stochasticity due to small population size (Lande 1993). In MLL-lake Hokajärvi, total consumption remained close to the level before pike removal, as the consumption of small-sized pike increased and compensated the decrease or absence of consumption of large pike, which were extinct by 2011 (Tiainen *et al.* 2017). In Majajärvi, where large pike also vanished in 2011, and pike population density and biomass decreased, pike consumption by all size-classes declined, reflecting the inability to recover from heavy exploitation by MLL.

Pike P/C was clearly positively affected in all lakes except Haukijärvi, as a response to removal fishing. This may indicate increased energy allocation on somatic growth as a result of released resources by decreased competition (Pierce and Tomcko 2003). Interestingly, small and medium-sized pike responded to fishing by increased P/C, but in large pike the P/C decreased, indicating decrease in growth. Unfortunately, we were not able to verify this observation by growth analysis, except in Majajärvi with 12 yr. old pike, since the number of large pike in age-groups >10 yr. were in general too low. Possible reasons to low growth of large pike include the environmental factors described earlier, and scarcity of energetically optimal prey size (Diana 1996). Growth of large pike was not positively affected by removal fishing, because their foraging possibilities are likely not much constrained by intraspecific or intraguild competition or risk of cannibalism due to their large size and low number (Raat 1988, Grimm and Klinge 1996). Large pike also use the pelagic area of the lake (Kobler *et al*. 2008, Pierce *et al*. 2013), which improves their foraging possibilities compared to smaller conspecifics. However, catch and release fishing (including tagging) has been reported to cause decreased growth for pike (Klefoth *et al*. 2011) and large pikeperch (Stålhammar 2013), which may have contributed to decreased growth or P/C in the largest pike in this study

4.4. Responses of prey fish populations on predation by pike

We did not observe a clear connection between pike consumption and prey fish population abundances, although pike consumption on perch was substantial, amounting to 30.8-60.4 % of the annual perch biomass in the study lakes. Although pike biomasses decreased at some extent in all study lakes (Tiainen *et al*. 2017), total consumption by the pike was compensated by increased growth rate, except in MLL-regulated Majajärvi. Also, increased P/C refers to improved capability of the pike population to allocate more energy to somatic growth. An exception to this was Majajärvi, where the pike population and its consumption collapsed, which enabled the increase of perch population. Responses in MLL-regulated Majajärvi reveal the importance of pike as a structuring force in lake ecosystems. Because of intensive fishing, the few remaining pike were able to consume annually less than 5 % of the

estimated perch biomass at the end of the study period, and the perch population was only little affected by predation by pike.

The ability of pike to affect to lower trophic levels is a well-established phenomenon (Carpenter and Kitchell 1993, Byström *et al*. 2007), and large pike has greater potential to digest prey species of diverse size, due to their larger gape size (Hart and Hamrin 1988, Nilsson and Brönmark 2000). Predation by pike has a strong structuring effect on prey fish populations by decreasing their number and controlling their behavior by predation threat (Persson *et al*. 1996, Skov *et al*. 2002, Estlander and Nurminen 2014). Pike population containing large individuals also have a stronger effect on prey fish populations, compared to pike population with truncated size distribution (Skov *et al*. 2002, Jolley *et al*. 2008). The removal of large pike is encouraged by Sharma and Borgstrøm (2008) in order to increase the total consumption by the pike population, as young and fast-growing pike are saved from cannibalism by larger pike. However, our results do not support that recommendation, as the decreased consumption of large pike may not be compensated by the consumption of smaller pike. According to our results, large pike had high consumption despite their low growth, and thus their conservation especially in lakes with high density of planktivorous or benthivorous fish is advised.

4.5. Conclusion

This study provides further evidence of the advantages of HSL compared to MLL. In HSL-lakes, production and consumption by pike were less affected than in MLL-lakes, as production and consumption were distributed on diverse sized pike. Our study is in line with the other recent studies (Arlinghaus *et al*. 2010, Matsumura *et al*. 2011, Gwinn *et al*. 2015), according to which protection of large individuals is encouraged to maintain the natural size and age structure, preserving trophy fish and maintaining long-term productivity of the fish population. With intermediate fishing pressure, harvested pike are compensated by increased recruitment and growth. The conservation of large pike by HSL maintains relative stability of pike production and consumption, thus remaining as a strong structuring force in the ecosystem.

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Appendix. *Average monthly (May-October) temperatures in the study lakes in years 2006-2013 used in the bioenergetic model. HSL = harvestable slot-length limit regulation, MLL = minimum length limit regulation.*

Lake	Month	2006	2007	2008	2009	2010	2011	2012	2013
Haarajärvi	May	10.7	11.1	12.0	11.7	6.5	10.7	11.6	13.7
(HSL)	June	17.3	18.0	16.8	16.1	15.0	18.4	16.2	19.4
	July	21.1	19.3	19.2	19.3	21.3	22.1	19.7	19.6
	August	19.2	19.1	17.1	18.5	17.7	18.6	18.1	18.7
	September	12.9	11.6	11.8	14.1	12.2	14.1	13.2	13.7
	October	10.0	9.5	7.0	6.5	8.2	9.8	6.0	7.4
Haukijärvi	May	6.6	10.4	10.3	11.4	6.5	10.8	10.3	12.9
(HSL)	June	14.6	16.9	15.2	14.8	15.0	17.8	13.1	17.9
	July	19.3	17.3	16.9	17.8	21.2	20.6	14.8	16.6
	August	19.9	17.0	14.1	17.3	17.2	18.5	15.2	15.4
	September	12.6	9.9	9.6	13.4	12.5	13.9	11.6	11.6
	October	10.0	6.7	7.0	7.1	8.0	10.1	7.0	7.0
Hokajärvi	May	8.0	12.5	13.3	12.5	7.4	7.6	13.9	13.3
(MLL)	June	19.3	18.2	17.5	15.7	15.0	17.4	16.6	19.4
	July	21.4	18.7	19.7	19.1	20.7	22.2	19.9	19.6
	August	20.4	18.2	17.0	17.6	17.5	19.2	18.4	18.7
	September	14.7	11.3	11.2	13.6	12.4	17.0	13.2	13.7
	October	10.0	8.8	7.0	7.0	7.8	10.3	6.0	7.4
Majajärvi	May	8.3	12.5	13.2	12.6	11.0	12.3	13.5	13.8
(MLL)	June	19.5	19.1	17.6	16.7	15.0	19.8	15.9	18.6
	July	22.0	20.3	19.8	19.7	22.7	22.9	19.3	18.5
	August	20.4	19.9	17.0	18.2	17.3	19.2	17.5	17.6
	September	14.5	11.4	11.3	13.6	12.8	14.4	12.2	12.7
	October	10.0	9.1	7.0	5.3	8.3	10.7	7.0	7.3

III

Pike (*Esox lucius*) diet in small boreal lakes based on stomach content analysis and stable isotopes

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Abstract

We investigated the changes in the diet and trophic position (TP) of pike in relation to changes in their abundance and growth rate determined by experimental fishing in four 2.1–13.8 ha, close to pristine forest lakes in southern Finland during 2006–2013. Stomach content analysis (SCA) and stable isotope analysis (SIA) of nitrogen and carbon were conducted. In the latter analysis, we also examined the applicability of SIA from fins as compared to muscle tissue. The results support the top predator status and the opportunistic nature of pike: they mainly preyed on fish according to their abundance, but their diet nevertheless included a wide range of taxa. The importance of benthic invertebrates decreased as a function of pike size, while the proportion of higher vertebrates (amphibians and mammals), as well as the TP, increased. We observed a connection between the results from SCA and SIA: invertivorous pike had a lower TP than exclusive fish eaters or individuals with an empty stomach. The importance of other prey than fish, and the relatively small prey size of large pike indicated the existence of resource limitation. We also found a negative effect of pike growth on the TP, which decreased during study period, even though the diet remained similar and the growth rate of pike increased. We detected a significant correlation between results from fin and muscle SIA samples. Therefore, pike do not need to be sacrificed to obtain reliable results for SIA. We recommend the cleaning of fin samples and the application of correction equations to further improve the comparability.

Keywords: Pike, *Esox lucius,* stomach contents, stable isotope analysis, trophic position

1. INTRODUCTION

As a top predator, pike (*Esox lucius*) affects the abundance and structure of prey fish populations directly by predation (Raat 1988, Craig 1996) and indirectly through predation threat (Lima & Dill 1990, Skov *et al*. 2007, Estlander & Nurminen 2014). Pike is a cannibalistic and kleptoparasitic species (Raat 1988, Craig 1996) and can regulate its own population dynamics (Andersson *et al*. 2007). Pike is an opportunistic, visually oriented ambush predator with a diverse diet (Bry 1996, Paradis *et al*. 2008). In addition to fish, pike can feed on invertebrates, amphibians, small mammals and waterfowl (Craig 1996). However, some studies have demonstrated individual specialism (Beaudoin *et al*. 1999, Amundsen *et al*. 2003), which may be related to behavioural traits such as activity, aggressiveness, explorativeness and boldness (Sih *et al*. 2004, Pasquet *et al*. 2016, Vainikka *et al*. 2016). Invertivory (i.e. feeding on macroinvertebrates) has even been reported in relatively large pike, although is considered to be energetically ineffective (Chapman *et al*. 1989, Diana 1996, Venturelli & Tonn 2006, Pedreschi *et al*. 2015). Pike has a large gape size, enabling it to ingest large prey (Hart & Hamrin 1988, Nilsson & Brönmark 2000). The prey size usually increases as a function of pike size (Frost 1954, Diana 1996).

Pike is a key species in small humic lakes (Tonn *et al.* 1990), which are common in the northern cold and temperate climate zone (Kortelainen 1999). These lakes are characterized by a high water colour due to humic substances, as well as strong temperature and oxygen stratification in the summer and winter (Rask *et al*. 1999. Previous studies have demonstrated that high concentrations of terrestrial dissolved organic carbon (t-DOC) suppress pelagic and benthic reproduction (Karlsson *et al*. 2009, Vadeboncoeur *et al*. 2008). Fish species diversity and the relative area of the littoral habitat are also limited (Tonn & Magnuson 1982, Rahel 1984). These challenging environmental and biotic conditions adversely affect pike growth (Raitaniemi 1995, Margenau 1995, Rask *et al*. 1999), due to intraspecific competition on low resources. Invertivory is common in these conditions, probably due to the limited availability of more energy-rich resources combined with competition pressure and predation threat (Rask *et al*. 1999, Vander Zanden & Vadeboncoeur 2002, Venturelli & Tonn 2006). As pike is an apex predator, changes in its diet can affect the whole ecosystem, but the effects of changes in pike abundance on its diet and hence on possible trophic interactions have been less studied.

The pike diet can be investigated by stomach content analysis (SCA), in which the occurrence and proportion of prey items in the stomach contents can be quantified, and their importance in the diet estimated (Hyslop 1980). SCA provides direct and specific information on the taxa ingested shortly before capture (Hyslop 1980, Beaudoin *et al*. 1999). However, the diet of pike varies at spatial and temporal scales and between individuals, increasing the variation in SCA (Chapman *et al*. 1989, Vander Zanden & Rasmussen 1999). The proportion of empty stomachs is typically high in the SCA of piscivorous pike, because fish are energy-rich, relatively easily digested prey, which reduces the feeding frequency and increases

the probability of having an empty stomach (Chapman *et al*. 1989, Paradis *et al*. 2008). Therefore, the proportion of empty stomachs has often been used as an index of piscivory (Chapman & Mackay 1990; Arrington *et al*. 2002). In addition, differences between prey items in the digestion rate may cause bias in SCA (Hyslop 1980). For example, the hard shells of some invertebrates and pharyngeal bones of roach may remain in the stomach for a long time after the ingestion of a prey animal (Vander Zanden & Vadeboncoeur 2002).

An alternative approach to assessing the dietary composition and trophic position (TP) in the ecosystem is stable isotope analysis (SIA) (Beaudoin *et al*. 1999, Syväranta 2008). Carbon and nitrogen are the most commonly used elements in SIA. In fish, the isotope values of muscle reflect the assimilated diet over up to one year, but are less specific than SCA from a taxonomic perspective (Syväranta 2008). Carbon isotopes are usually used to trace the energy sources in the trophic web (Post 2002, Syväranta 2008). Carbon fractionates very little, with an average fractionation of only 0.4‰ (Post 2002), although variation may occur (Taipale *et al*. 2016). The isotopic signature of carbon differs between littoral and pelagic food webs, which can be used to trace the origin of carbon in an organism (Vander Zanden & Vadeboncoeur 2002). The nitrogen isotope ^{15}N fractionates more than carbon, with an average fractionation of 3.4‰ for each trophic level (Post 2002), and this can be used to determine the trophic position of an organism (Post 2002, Syväranta 2008).

Muscle tissue has traditionally been used in SIA (hereafter muscle SIA), but it usually requires the studied organism to be sacrificed (for biopsy of living pike, see Baker *et al*. 2014 and Van Walleghem *et al*. 2013). This is not desirable when studying endangered species (Jardine *et al*. 2011, Sanderson *et al.* 2009) or other fish for conservation purposes, such as large predators (Birkeland & Dayton 2005, Arlinghaus *et al*. 2010, Kuparinen *et al*. 2016). SIA from fin clips (hereafter fin SIA) is a promising, non-lethal sampling method, as the isotopic signature of fin samples differs only slightly from that of white muscle tissue (Kelly *et al*. 2006, Sanderson *et al*. 2009). Despite the small difference, fin SIA may require a correction factor to obtain comparable $\delta^{13}C$ and $\delta^{15}N$ values to muscle SIA (Kelly *et al*. 2006). Fin SIA has been used to determine the TP in pike (Syväranta *et al*. 2010), but the correspondence between fin SIA and muscle SIA for pike has not so far been examined.

In this study, we estimated the frequency of invertivory in pike of different sizes, and the effects of size-selective fishing (minimum length limit, MLL ≥ 40 cm or harvestable slot-length limit, HSL 40–64.9 cm, see Tiainen *et al*. 2017) on the diet and trophic status of pike in four study lakes. We also assessed the reliability of $\delta^{13}C$ and $\delta^{15}N$ values in fin SIA samples for determining the TP. Our hypotheses, based on the literature described above and on our earlier studies (Tiainen *et al*. 2017 and Tiainen *et al.* unpublished), were as follows:

1) Due to interspecific competition, predation avoidance and their smaller gape size, the diet of small pike includes relatively higher proportion of benthic invertebrates compared to larger individuals, but the proportion of

fish in the diet and the TP increase as a function of pike size. Furthermore, the proportion of larger prey, namely fish, amphibians and mammals, increases as a function of pike length.

2) If SCA reflects the long-term piscivorous diet of pike, those pike that have only fish in their stomach or have an empty stomach should have a higher TP than pike that have consumed macroinvertebrates.
3) As a result of decreased competition and released resources resulting from pike removal, the importance of fish in the pike diet increased in small and young fish at a smaller size and age from 2008–2009 to 2013, which increased the TP of pike.
4) Similarly to other studied species, the isotopic signatures of C and N in pike fins are close to the equivalent values from muscle tissue, and can be used in SIA without sacrificing the fish.

The results of this study could help in understanding how the role of pike in the ecosystem varies in relation to their size and fishing pressure. The study also increases our knowledge of how the exploitation of pike populations may affect the TP and the ability of pike to control prey species in the ecosystem. Finally, if fin SIA appears to be comparable with muscle SIA, it will help in the development of non-lethal sampling techniques, thus avoiding the unnecessary sacrifice of fish.

2. MATERIAL AND METHODS

2.1 Study lakes

This study was conducted in four small (2.1–13.8 ha) forest lakes in southern Finland (61° 13' N; 25° 12' E). The study lakes are nearly pristine with a catchment area mainly consisting of coniferous forest and peatlands. The lakes are reserved for research use only, and are not subjected to agricultural or industrial pollution. They are oligo-mesotrophic, have a low pH and are coloured by humic substances. The long-term mean water colour is 130 and 140 mg Pt l^{-1} in the less humic lakes Hokajärvi and Haarajärvi, and 330 and 340 mg Pt l^{-1} in the more humic lakes Haukijärvi and Majajärvi (Estlander *et al*. 2010). The lakes display strong temperature and oxygen stratification during the summer, as well as a naturally low oxygen content (excluding Haarajärvi) in the hypolimnion during summer and winter stratification. Although these conditions are normal for small humic lakes (Rask *et. al*. 1999), they have a profound effect on the fish community and whole ecosystem.

In all of the study lakes, the dominant fish species are perch, roach and pike. Other species include bream (*Abramis brama*) in Hokajärvi and Haukijärvi, bleak (*Alburnus alburnus*) in Hokajärvi, burbot (*Lota lota*) in Haarajärvi and Hokajärvi, introduced whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in Haarajärvi and introduced tench (*Tinca tinca*) in Majajärvi (Olin *et al*. 2010). The macroinvertebrate community of the lakes includes many large-sized taxonomic groups (such as the water flea, *Asellus aquaticus*, and larvae of mayflies, Ephemeroptera, and dragonflies, Anisoptera), which are suitable prey for pike (Estlander *et al*. 2010).

2.2 Data collection

An extensive research programme was conducted in the four study lakes in 2005–2013, including size-selective pike removal in 2008–2012. The research programme covered fish populations, macroinvertebrates, zooplankton, macrophytes and water quality (Estlander *et al*. 2009, Estlander *et al*. 2010, Horppila *et al*. 2010, Olin *et al*. 2010). During pike removal, on average 31.6 and 54.7% of the estimated population of pike ≥35 cm in length were annually removed from the HSL lakes Haarajärvi and Haukijärvi, and 39.6 and 60.4% from the MLL lakes Hokajärvi and Majajärvi (Tiainen *et al*. 2017). All pike were measured for length (nearest mm), weighed, aged and analysed for back-calculated growth (chleithrum bone: linear growth model, Casselman 1990; or scales: Fraser-Lee equation, Frost and Kipling 1959) by 1–2 experienced readers.

Samples (n = 542, length range 8.4–96.1 cm, age range 0–19 yr.) for stomach analyses were collected as part of the pike monitoring and removal programme in 2005–2013. Pike were mainly caught using fyke nets (n = 161), bait fishing through the ice cover (n = 24) in April to early May, experimental gillnetting (CEN 2005, Olin *et al*. 2010) in July to August (n = 72) and angling (n = 265) in late summer and autumn. The fyke nets had a large mesh size (30 mm from knot to knot), thus not catching small prey fish, and pike were not observed to feed while retained in the gear. The rest of the pike (n = 20) were caught by other methods (spring-loaded fish hooks, fish spear or long line) or found dead (see Tiainen *et al.* 2017 for detailed sampling methods). Muscle SIA samples were taken from a sub-sample of the pike captured for stomach analyses in 2008–2009 (n = 190) and in 2013 (n = 58). Fin SIA samples were taken from released individuals (n = 81) during pike monitoring in 2008–2009 and, to enable a comparison between muscle and fin SIA, as a sub-sample of pike killed for stomach and muscle SIA analyses (n = 60).

To obtain SIA data from the prey species of pike and to determinate the basic SIA value in the littoral and pelagic zones, the isotopic values of the most abundant fish, invertebrates and zooplankton were determined (Table 1). From the most important prey species of pike, i.e. perch and roach, SIA samples were collected (from the wire trap and gillnet catch) in spring (n = 103 for perch, n = 96 for roach) and summer 2009, (n = 119 for perch, n = 96 for roach) and in summer 2013 (n = 24 for perch, n = 24 for roach). For muscle SIA, a roughly 1 x 2 cm piece of white and boneless muscle tissue was prepared from the dorsal side of the sampled fish. SIA samples from pike fins (ca. 1/3 from the tip of the right or left pelvic fin, depending on the year) were halved. One half was not purified, while the other half was cleaned by rinsing the fin for two minutes in a petri dish with 1.2 M HCl. After the acid treatment, the fin halves were rinsed in purified water in a line of six petri dishes, whose water was changed after every four samples or when impurities were visible. Benthic invertebrates were collected from each study lake from three distinct littoral sampling areas by kick netting or by hand picking in spring and summer 2009, and were sorted according to the species or species group (*Asellus aquaticus*, *Anisoptera*, *Ephemeroptera*). Invertebrates were kept alive in a refrigerator until the next morning to empty their intestines (Mateo *et al*. 2008). Zooplankton samples were collected in July to August 2009 using a 180-µm

plankton net with vertical lifts and sorted into cladocerans and copepods. All the stomach and SIA samples were stored in a freezer at -20 °C before further preparation and analyses.

Table 1. Number of SIA samples from pike (muscle and fin SIA), and roach and perch (only muscle SIA) from the study lakes in 2008, 2009 and 2013. The fin SIA sample marked with an asterisk is a sub-sample from pike sampled for muscle SIA to enable a comparison of $\delta^{13}C$ and $\delta^{15}N$ values of fin and muscle tissue from the same fish.

Lake	Species	Sample	2008	2009	2013
Haarajärvi	Pike	Muscle SIA	19	60	24
		Fin SIA		57	
		Fin SIA*		30	
	Roach	Muscle SIA		54	6
	Perch	Muscle SIA		68	6
Haukijärvi	Pike	Muscle SIA	1	10	6
		Fin SIA		5	
	Roach	Muscle SIA		43	6
	Perch	Muscle SIA		36	6
Hokajärvi	Pike	Muscle SIA	16	60	16
		Fin SIA		14	
		Fin SIA*		30	
	Roach	Muscle SIA		51	5
	Perch	Muscle SIA		62	6
Majajärvi	Pike	Muscle SIA		24	
		Fin SIA		5	12
	Roach	Muscle SIA		44	6
	Perch	Muscle SIA		56	6

2.3 Pike dietary analysis

In dietary analysis, prey items were taxonomically sorted and counted. Fish were measured to the nearest 1 cm. Stomach fullness was assessed using a points method (Hynes 1950, Windell, 1971, Hyslop 1980) with a scale of 0–12 applied for each prey item separately (0 = empty stomach and 12 = maximum fullness, all prey items together). Although this method is based on subjective visual assessment of fullness and is thus susceptible to different results depending on the viewer unless carefully assessed, the method is rapid and easy to apply (Windell 1971, Hyslop 1980). The possible between-year and between-lake differences in the stomach contents were analysed with MANOVA including the independent variables lake, year (2005–2007 pooled due to small sample sizes, and separate years from 2008 to 2013) and pike length class (<30, 30–39, 40–64, ≥65 cm), as well as all their interactions. The dependent variables included the arcsin-transformed fullness of different food items, including perch, roach, pike, other fishes, unidentified fishes, amphibians, mammals and macroinvertebrates. To determine the importance of different prey items in the pike diet, the indexes of absolute importance (*AI*) and relative importance (*RI*) by Hyslop (1980) were calculated for each prey item. *AI* was calculated using the equation:

$$AI_i = O_{\%} + F_{\%} + N_{\%},$$

in which $O_{\%}$ is the percentage occurrence, $F_{\%}$ is the percentage of the total volume and $N_{\%}$ is the proportion of a prey item in the total count of prey items. *RI* was calculated using the equation:

$$RI = 100\ x\ \frac{AI_i}{\sum_{i=1}^{n} AI_i}$$

2.4. Stable isotope analysis

All isotopic samples from 2008–2009 were oven dried at 65 °C for 48 h. Pike muscle SIA samples from 2013 were freeze dried in a Savant ModulyoD Freeze Dryer for 48 h at -50 °C. All samples were ground to a fine powder, and 0.25–0.6 mg (1 µg accuracy) of the powder was weighed into small tin capsules. All SIA samples from 2008 and 2009, and roach and perch samples from 2013, were analysed for $\delta^{13}C$ and $\delta^{15}N$ fractions using an isotope ratio mass spectrometer (Thermo Finnigan Delta^{plus} Advantage) with a FlashEA 1112 elemental analyser in the Department of Bio- and Environmental Sciences of the University of Jyväskylä. Pike muscle SIA samples from 2013 were analysed with the same mass spectrometer model coupled to an NC 2500 elemental analyser in the Laboratory of Chronology of the Finnish Museum of Natural History. All isotope results are presented in relation to international standards (Vienna PeeDee Belemnite for C and atmospheric nitrogen for N). No differences were detected in the SIA values of pike for 2008 and 2009 (ANCOVA including the dependent variables lake, year and pike length), and the data for these two years were therefore pooled. The differences in SIA values between species, lakes and years were analysed with a general linear model (GLM) including $\delta^{13}C$ or $\delta^{15}N$ as an independent variable, and species (pike, perch, roach), lake (Haukijärvi, Majajärvi, Hokajärvi, Haarajärvi), year (2008–2009 vs. 2013), length of species (continuous), and all their interactions as dependent variables. The best model was chosen based on Akaike's information criterion.

The trophic position (TP) of pike, roach and perch was calculated using the following equation by Post (2002): $TP = \lambda + (\delta^{15}N_{sc} - \delta^{15}N_{base})/ \Delta_n$, where λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$ (e.g., $\lambda = 1$ for primary producers), $\delta^{15}N_{sc}$ is the measured $\delta^{15}N$ value of a secondary or higher consumer, and Δ_n is the enrichment in $\delta^{15}N$ per trophic level. In this case, a value of 3.4 was used (Post 2002). The effects of lake, year, length and growth (measured as length increment (LI) in the previous year) on TP were analysed using a GLM model. Length and LI were ln-transformed to obtain a normal distribution.

To establish a comparable baseline for the trophic positions of pike, perch and roach in different lakes, trophic levels were scaled according to *Asellus aquaticus* with TP of 1, because long-living molluscs and bivalvia, which are commonly used as a baseline (Syväranta 2008), are scarce in the study lakes.

To assess the effects of stomach contents on the TP of pike, those pike for which both stomach and SIA data were available were divided into four stomach

categories: empty stomach (n = 100), macroinvertebrates in the stomach (n = 13), only fish in the stomach (n = 129) and amphibians in stomach (n = 5, no mammals were recorded in the stomachs of these pike). The effects of the stomach category, lake and year (and all their interactions) were analysed with ANOVA.

3. RESULTS

3.1. Pike diet

Of the 542 stomachs analysed, 265 contained food and 277 (51.1%) were empty. The probability of having an empty stomach was not dependent on pike length. Altogether, 15 different food items were identified, including six fish species, four macroinvertebrate species and 2 species of amphibians and mammals (Table 2).

Table 2. Prey items found in pike stomachs, and the number of pike stomachs they were present in (n_{pike}), relative proportions (RP), occurrence (O), numbers of prey items eaten (n_{prey}), proportions of the total number of individual prey (n%) and indexes on absolute importance (AI) and relative importance (RI).

Prey item	Prey item	n_{pike}	*RP*	*O*	n_{prey}	*n%*	*AI*	*RI*
Fishes	*Rutilus rutilus*	137	0.46	0.52	204	0.41	142.79	45.21
	Perca fluviatilis	112	0.35	0.42	154	0.31	108.88	34.47
	Esox lucius	10	0.05	0.04	11	0.02	11.89	3.76
	Alburnus alburnus	1	0.00	0.00	1	0.00	1.06	0.34
	Abramis brama	1	0.01	0.00	1	0.00	1.54	0.49
	Coregonus albula	1	0.01	0.00	1	0.00	1.51	0.48
	Unidentified fish	15	0.01	0.06	3	0.01		
Amphibian	*Rana* sp.	7	0.02	0.03	9	0.02	6.36	2.01
	Lissotriton vulgaris	1	0.00	0.00	1	0.00	0.77	0.24
Mammals	*Neomys fodiens*	3	0.01	0.01	3	0.01	2.32	0.73
	Arvicola amphibius	3	0.01	0.01	2	0.00	2.79	0.88
Macro-	*Asellus aquaticus*	17	0.04	0.06	56	0.11	18.43	5.84
invertebrates	*Ephemeroptera* larvae	5	0.00	0.02	43	0.09	10.99	3.48
	Anisoptera larvae	6	0.00	0.02	7	0.01	4.21	1.33
	Anisoptera adult	2	0.00	0.01	1	0.00	1.15	0.36
	Astacus astacus	1	0.01	0.00	1	0.00	1.16	0.37
	Unidentified macroinv.	6	0.01	0.02	1	0.00		
	Sum	328	1.00	1.24	499	1.00	315.85	100.00

Of all pike with non-empty stomachs, 97% had consumed fish, 10% macroinvertebrates, 3% amphibians and 2% mammals. Most (89.4%) pike had only consumed one type of food item, 10.2% had two types and 0.3% had three different food items. Of the pike that had fed on macroinvertebrates, 26% had also consumed fish. Half of the pike that had fed on amphibians had also consumed fish.

In terms of fullness, the food in pike stomachs mainly consisted of fish (93% of the total fullness, Fig. 1) and to a lesser extent macroinvertebrates (3%), amphibians (2%) and mammals (1%). The probability of invertivory decreased as a function of pike size, but not significantly (logistic regression: Wald $X^2_{1,1} = 3.064$, $p = 0.080$, Fig. 1). The probability of consuming amphibians or mammals increased strongly in large pike (logistic regression: Wald $X^2_{1,1} = 13.047$, $p < 0.001$). Roach and perch were clearly the most important food items (Fig. 2), and they comprised 84% of the total volume of stomach contents. According to the RI, roach was more important food item than perch (Table 2). No significant between-year or between-lake differences (MANOVA) were observed in the pike diet (Fig. 2).

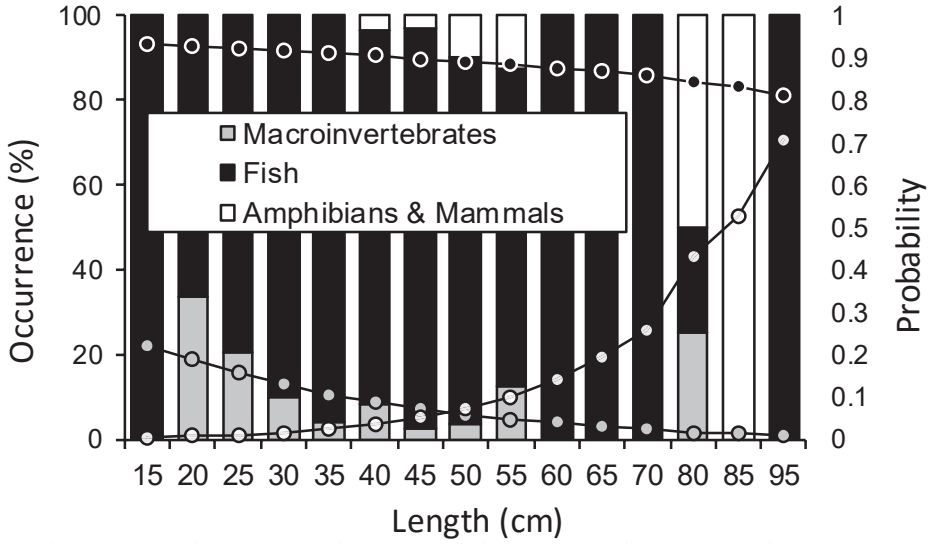

Fig. 1. The observed occurrence of macroinvertebrates (grey bars), fish (black bars) and amphibians and mammal (white bars) in pike stomachs containing food items, and modelled probability from logistic regression of fish (black dotted line), macroinvertebrates (grey dotted line) and amphibians and mammals (white dotted line) occurring in pike stomachs.

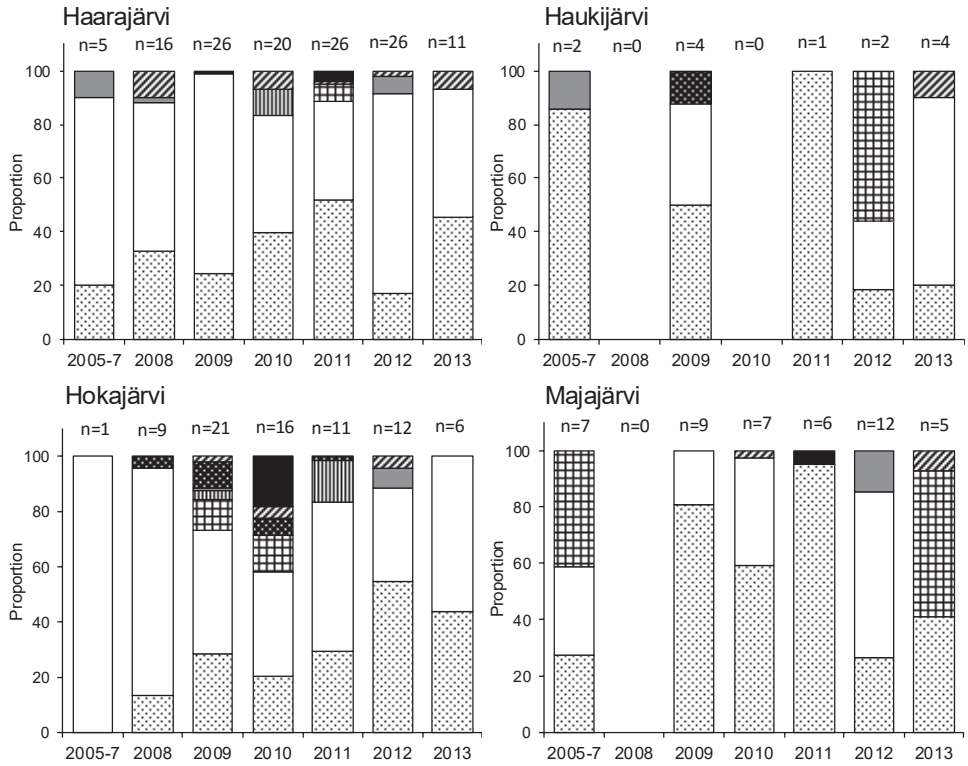

Fig. 2. Proportions of prey items (white = roach, black-dotted pattern = perch, grid pattern = pike, vertical pattern = other fish, grey = unidentified fish, white-dotted pattern = amphibians, black = mammals, diagonal pattern = macroinvertebrates) in pike stomachs in the study lakes in 2005–2013. The years 2005–2007 are combined. The number of non-empty stomach samples is indicated above the columns.

The size of prey increased significantly as a function of pike size (linear regression: $r^2 = 0.105$, $F_{1,292} = 34.19$, $p < 0.001$), but the variation was high and the largest ingested prey (≥20 cm) were mainly caught by mid-sized (40–55 cm) pike (Fig. 3). Individuals <25 cm in length had not fed on prey with a size of >10 cm, while the stomach contents of >65 cm pike did not include prey <8 cm in size. A large proportion of the prey size variation was dependent on the prey species, and the model including prey species explained a considerably greater amount of the variation (ANCOVA: $r^2 = 0.279$, $F_{1,285} = 13.82$, $p < 0.001$). The prey species had a significant effect ($p < 0.001$) on the relationship between predator pike size and prey size, and perch were consumed at smaller size (average 9.1 cm) than roach (average 10.3 cm) or pike (14.2 cm). Prey size as a proportion of pike size was on average 22.9% (range 8.7–51.3%), but decreased as a function of pike size (linear regression: $r^2 = 0.176$, $F_{1,292} = 62.34$, $p < 0.001$). Pike larger than 65 cm had not fed on perch but mainly on roach.

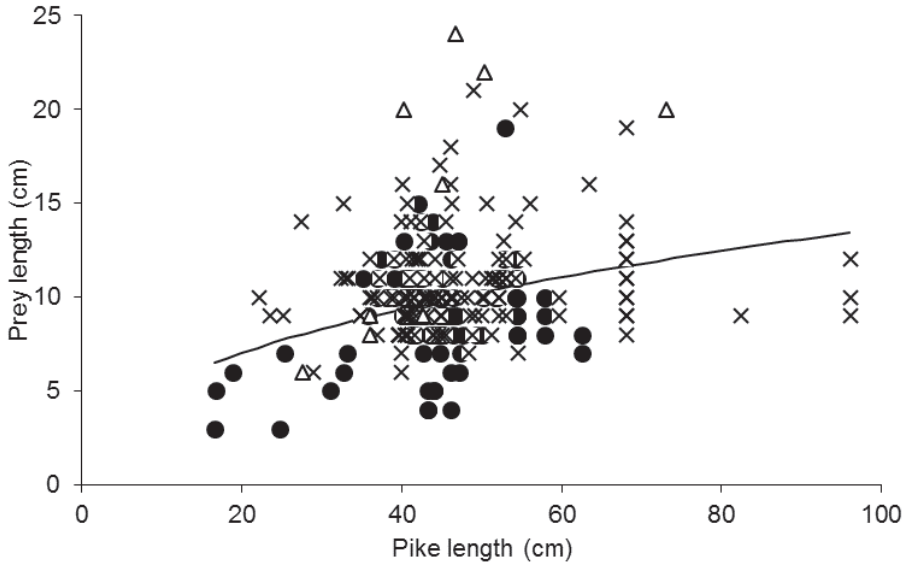

Fig. 3. Size of prey fish in relation to pike size. Different symbols refer to separate prey species: black dots = perch, crosses = roach, white triangles = pike. The black line refers to the fitted regression from the model.

3.2. Fin SIA in relation to muscle SIA

The $\delta^{13}C$ and $\delta^{15}N$ values of both the uncleaned and purified fin SIA samples correlated significantly with the corresponding values for muscle SIA samples (Fig. 4). However, the $\delta^{13}C$ values of the fin SIA were higher than muscle SIA values (ANOVA: $F_{2,177} = 10.99$, $p < 0.001$) for both cleaned and uncleaned fin samples (Tukey: $p = 0.003$ and $p < 0.001$, respectively). Cleaning reduced the average difference between muscle and fin $\delta^{13}C$ values from 4.2% to 2.8%. The $\delta^{15}N$ values in muscle and cleaned or uncleaned fin samples did not differ significantly (ANOVA: $p > 0.100$). However, the intercept in the regression between muscle and fin samples significantly differed from zero ($p = 0.038$ and 0.076 for uncleaned and cleaned fin samples, respectively), indicating larger differences for higher $\delta^{15}N$ values (Fig. 4). Therefore, and because of the high δ13C values in fin SIA samples, the following equations were used to correct the fin SIA values of released pike to be comparable with the muscle SIA values in the further analyses:

(1) $\delta^{13}C_{muscle} = 0.967*\delta^{13}C_{fin\_uncleaned} - 2.207$, $R^2 = 0.900$, $F_{1,58} = 523.509$, $p < 0.001$

(2) $\delta^{13}C_{muscle} = 0.953*\delta^{13}C_{fin\_purified} - 2.207$, $R^2 = 0.908$, $F_{1,58} = 573.559$, $p < 0.001$

(3) $\delta^{15}N_{muscle} = 0.882*\delta^{15}N_{fin\_uncleaned} + 1.031$, $R^2 = 0.840$, $F_{1,58} = 303.408$, $p < 0.001$

(4) $\delta^{15}N_{muscle} = 0.917*\delta^{15}N_{fin\_purified} + 0.721$, $R^2 = 0.893$, $F_{1,58} = 482.082$, $p < 0.001$

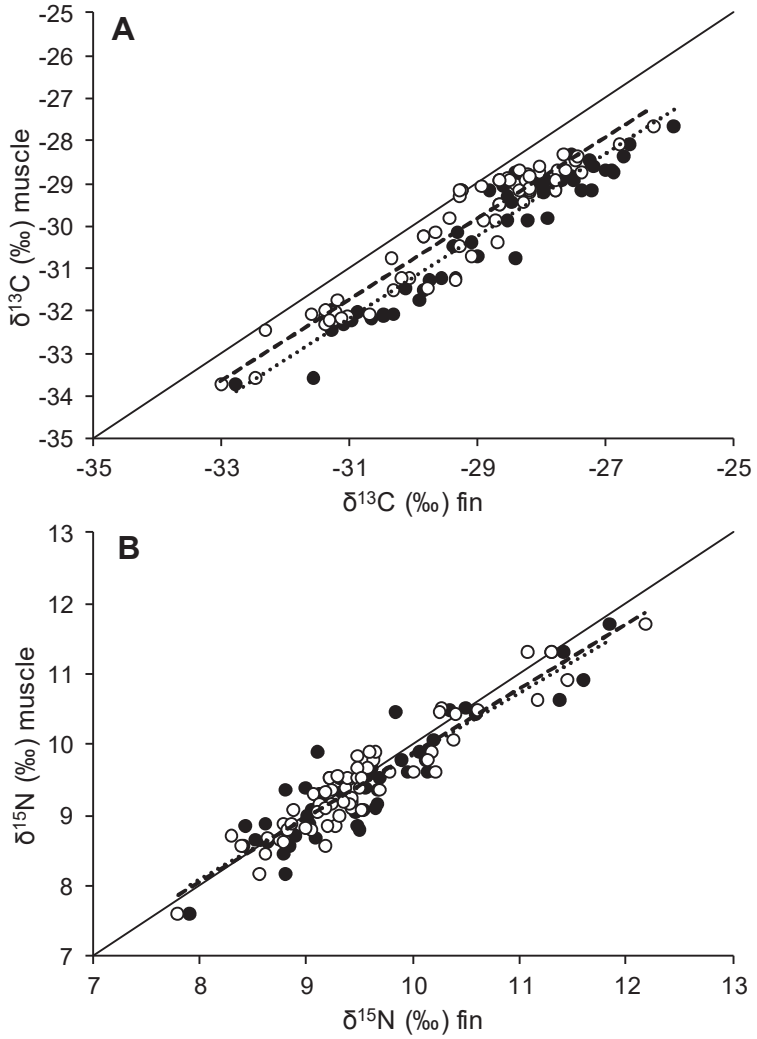

Fig. 4. The $\delta^{15}N$ and $\delta^{13}C$ values from purified (white dot) and non-purified (black dot) fin samples in relation to the corresponding muscle values in pike. Dotted and dashed lines represent regressions fitted to values from purified and non-purified fin or muscle values, respectively. Diagonal solid lines describe the hypothetical equal values for fin and muscle samples.

3.3. Pike SIA values in relation to different trophic categories and years

Pike had the highest $\delta^{15}N$ values of all trophic categories and were at the top of the food web in all of the lakes in most of the years (Fig. 5). On average, pike $\delta^{15}N$ values were 1.31‰ and 0.78‰ higher compared to roach and perch, respectively (Table 3, Tukey: $p < 0.001$ in both cases). Exceptionally, in 2013 in Majajärvi, pike $\delta^{15}N$ values were below those of perch, but did not differ significantly (Tukey: $p = 0.151$). In the same year in Lake Haukijärvi, the $\delta^{15}N$ values of all three species

were very similar and did not differ significantly (Tukey: $p > 0.100$ in all cases). In all three species, $\delta^{15}N$ values decreased from 2008–2009 to 2013 (Tukey: $p < 0.001$–0.007). In pike, the average reduction (9.8%) was greater than in perch (8.2%) or roach (5.5%), except in Hokajärvi, where the reduction was greatest in perch. As a result, the average $\delta^{15}N$ values of pike, which in 2008–2009 were 0.91‰ and 1.57‰ higher than the corresponding values of perch and roach, were only 0.66‰ and 1.05‰ higher in 2013.

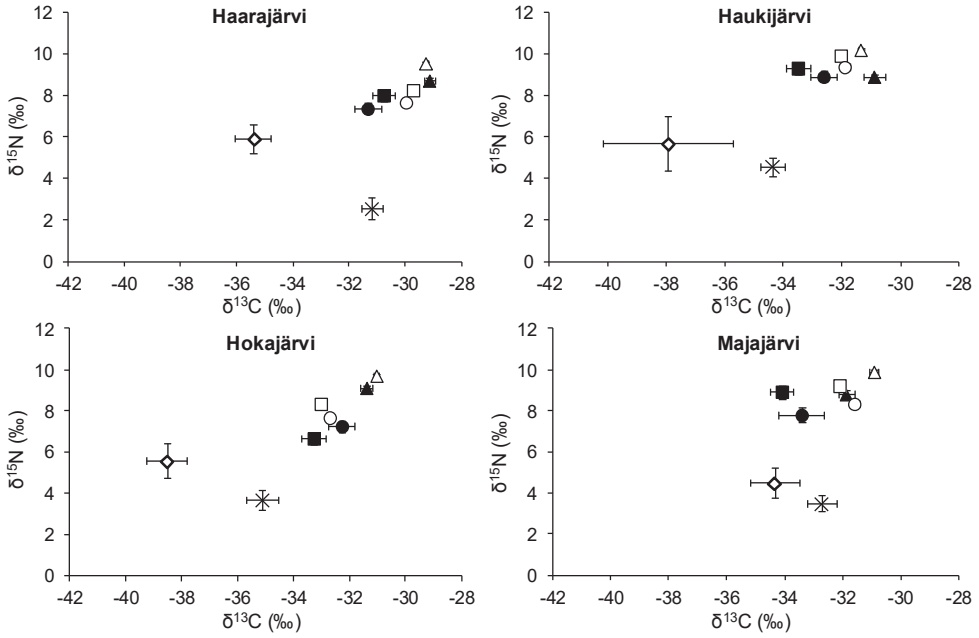

Fig. 5. Stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of different trophic categories in the study lakes: asterisk = macroinvertebrates, diamond = zooplankton, circle = roach, square = perch, triangle = pike. White symbols (and asterisks) represent values in 2008–2009, and black symbols those in 2013. In fish, SIA values represent average-sized individuals: 14 cm perch and roach, and 42 cm pike. Error bars denote the standard error (SE).

The $\delta^{13}C$ values in pike, as well as in roach and perch, were closer to invertebrate than zooplankton values, indicating that a major part of the carbon in pike originates from littoral sources (Fig. 5). An exception was 2013 in Majajärvi, where the $\delta^{13}C$ values in perch were closer to zooplankton than to macroinvertebrates. The $\delta^{13}C$ values in pike were closer to roach than to perch, except in Haarajärvi. In perch, the $\delta^{13}C$ values decreased from 2008–2009 to 2013 (Table 4, Tukey: $p < 0.001$–0.024), except in Hokajärvi (Tukey: $p > 0.100$). In roach, the $\delta^{13}C$ values were lower in 2013 compared to 2008–2009 in Haarajärvi and Majajärvi (Tukey: 0.017 and 0.022, respectively) but not in Haukijärvi or Hokajärvi. In pike, the $\delta^{13}C$ values only differed between years in Majajärvi (Tukey: $p = 0.0023$), where the values decreased. As a result of above changes, the differences in the $\delta^{13}C$ values between the species were higher in 2013 than in 2008–2009, except in Hokajärvi.

Table 3. Results of the GLM model for differences in $\delta^{15}N$ between lakes, years and species, and their interactions. Significant p-values are marked with asterisks.

Source	DF	SS	MS	F	p
Length	1	2.296	2.296	5.640	0.018*
Species	2	3.199	1.599	3.930	0.020*
Lake	3	1.669	0.556	1.370	0.252
Year	1	3.389	3.389	8.320	0.004**
Length*Species	2	1.538	0.769	1.890	0.152
Length*Lake	3	1.482	0.494	1.210	0.304
Species*Lake	6	6.367	1.061	2.610	0.017*
Length*Year	2	1.832	0.916	2.250	0.106
Species*Year	3	2.230	0.743	1.820	0.141
Lake*Year	6	6.536	1.089	2.670	0.014
Length*Species*Lake	1	0.139	0.139	0.340	0.560
Length*Species*Year	2	1.480	0.740	1.820	0.163
Length*Lake*Year	3	2.462	0.821	2.010	0.110
Species*Lake*Year	6	3.584	0.597	1.470	0.187
Length*Species*Lake*Year	6	5.767	0.961	2.360	0.029*

Table 4. Results of the GLM model for differences in $\delta^{13}C$ between lakes, years and species, and their interactions. Significant p-values are marked with asterisks.

Source	DF	SS	MS	F	*p*
Length	1	10.616	10.616	11.220	0.001**
Species	2	22.520	11.260	11.900	<0.001***
Lake	3	64.960	21.653	22.890	<0.001***
Year	1	7.220	7.220	7.630	0.006**
Length*Species	2	19.179	9.589	10.140	<0.001***
Length*Lake	3	15.263	5.088	5.380	0.001**
Species*Lake	6	19.469	3.245	3.430	0.002**
Length*Year	1	18.489	18.489	19.540	<0.001***
Species*Year	2	4.001	2.001	2.110	0.121
Lake*Year	3	21.231	7.077	7.480	<0.001***
Length*Species*Lake	6	25.109	4.185	4.420	<0.001***
Length*Species*Year	2	15.842	7.921	8.370	<0.001***
Length*Lake*Year	3	14.240	4.747	5.020	0.002**
Species*Lake*Year	6	8.958	1.493	1.580	0.151
Length*Species*Lake*Year	6	14.914	2.486	2.630	0.016*

3.4. Pike trophic position (TP) in relation to length and growth

The TP of pike increased significantly as a function of length (Fig. 6, Table 5). On average, pike with a length of 20, 40, 60 and 80 cm had a respective TP of 3.60, 4.00, 4.24 and 4.40. The lake had a significant effect, and the lowest average TP in 40 cm pike was observed in Haukijärvi (3.86) and the highest in Haarajärvi (4.28). The year also had an effect: the TP in 40 cm pike was on average 4.05 in 2008–2009, while it was 3.93 in 2013. Pike growth had a small negative effect, and when considering 40 cm pike, the individuals with an LI of 2.9 cm (half of the average) had on average a 1.47% higher TP (4.03) than the individuals (TP = 3.97) with an LI of 11.7 cm (twice as high as the average).

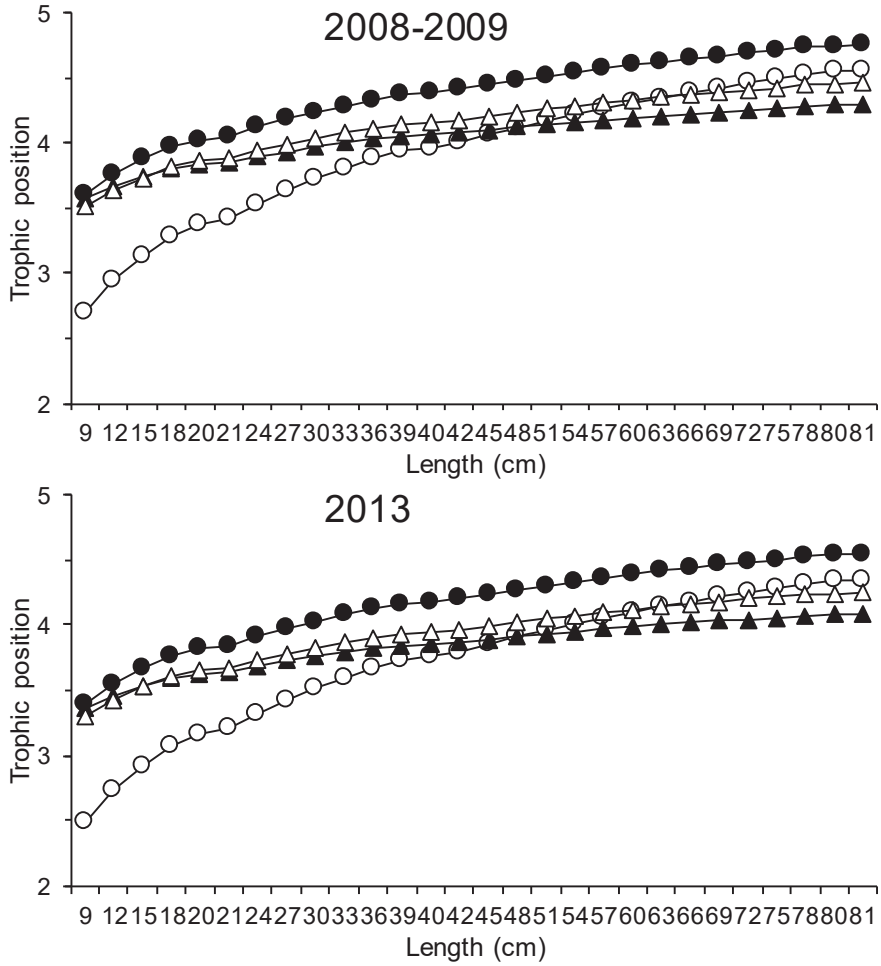

Fig. 6. The estimated trophic position in relation to pike length in the study lakes in 2008–2009 (A) and 2013 (B). Black and white dots refer to Lakes Haarajärvi and Haukijärvi and black and white triangles to Lakes Hokajärvi and Majajärvi, respectively.

Table 5. Results of the GLM model for the effects of lake, year, length and length increment (LI) and their interactions on the trophic position of pike. Only statistically significant interactions are presented.

Source	DF	Type III SS	MS	F	*p*
lnLength	1	4.415	4.415	165.89	<.0001
lnLI	1	0.088	0.088	3.29	0.071
Lake	3	0.783	0.261	9.81	<.0001
Year	1	1.944	1.944	73.06	<.0001
lnLength*Lake	3	0.615	0.205	7.70	<.0001
lnLI*Lake	3	0.346	0.115	4.34	0.005

3.5. SIA results vs stomach results

All of the studied variables, i.e. the stomach category, lake and year, significantly affected the TP of pike, and the interaction of lake*stomach category was also significant (Table 6, Fig. 7). The stomach category "macroinvertebrates in the stomach" had the lowest average TP (3.86) and differed significantly from the TP in the category "only fish in the stomach, TP = 4.08", and almost significantly from the category "empty stomach, TP = 4.02" (Tukey = 0.009 and 0.055, respectively). TP was highest in Haarajärvi (Tukey: $p < 0.001$ in all between-lake comparisons) and similarly high in the categories empty, macroinvertebrates and only fish in the stomach (no amphibians were detected in pike stomachs in Haarajärvi). In the other lakes, the TP of pike with macroinvertebrates in their stomachs was lower, although not significantly, in all cases compared to pike with only fish in the stomach (Tukey: $p = 0.038$, 0.003 and 0.328 for Haukijärvi, Hokajärvi and Majajärvi, respectively) or with an empty stomach (Tukey: $p = 0.195$, 0.001 and 0.591 for Haukijärvi, Hokajärvi and Majajärvi, respectively). The pike with amphibians in their stomachs had the second lowest average TP (3.99), but did not differ significantly from the other stomach categories.

Table 6. Results of the ANOVA model for the effects of stomach category, lake, year and their interaction on the trophic position of pike.

Source	DF	SS	MS	F	*p*
Stomach category	3	0.415	0.138	2.670	0.049
Lake	3	3.822	1.274	24.560	<.001
Year	1	3.016	3.016	58.140	<.001
Stomach category*Lake	8	0.912	0.114	2.200	0.029

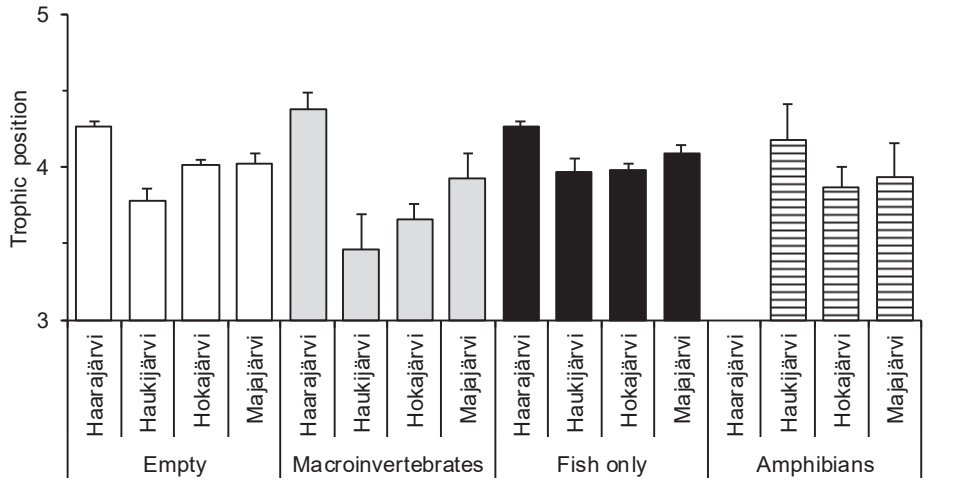

Fig. 7. The estimated trophic position of pike with different stomach contents (empty stomach, macroinvertebrates in the stomach, only fish in the stomach, and amphibians in the stomach) in the study lakes. Error bars denote the standard error.

4. DISCUSSION

The importance of benthic invertebrates in the diet decreased as a function of pike size, as we hypothesized. Conversely, the proportion of higher vertebrates (amphibians and mammals) and the trophic position increased as a function of pike size. We also found that stomach content analysis (SCA) does reflect the long-term diet in pike. This was demonstrated by the fact that the trophic position (TP) of pike with macroinvertebrates in the diet was lower than in exclusive fish eaters or in individuals with empty stomach. In contrast to our hypotheses, the importance of fish or the TP of pike did not increase in small and young individuals after the removal of pike from the study lakes. Carbon and nitrogen stable isotope values from fin samples were rather similar to the values from muscle samples, as we hypothesized, thus enabling SIA to be performed without sacrificing pike individuals.

4.1 Pike diet based on stomach content analysis

SCA revealed a diverse selection of prey items dominated by a few species. This is in accordance with previous studies on the opportunistic feeding of pike suggesting that pike feed on prey items according to their abundance, but their diet may still consist of a wide range of taxa (Frost 1954, Diana 1979, Kahilainen & Lehtonen 2003). The occurrence and fullness analyses clearly demonstrated that fish comprised the main prey for pike in these small, humic lakes. Fish were found in almost every non-empty stomach, which is typical for pike (Craig 1996, Vander Zanden *et al*. 1997, Kahilainen & Lehtonen 2003). Pike mainly fed on one prey item at a time, and the reliance on one type of prey (89.4%) was greater than in a

previous study by Diana (1979, 61%). This reflects the habit of pike of feeding on and digesting one fish at a time (Diana 1979), and also the low number of prey (fish) species in the study lakes. Roach and perch were the most important prey fish species for pike, reflecting the fish species composition in the lakes (Olin *et al*. 2010). Unfortunately, we could not establish whether pike selected roach over perch due to the lack of density estimation data for roach. However, the greater importance of roach in the pike diet and the ability to eat larger roach than perch indicate that pike might favour roach. Prey selection in pike is defined by the gape size and prey morphology (Hambright *et al*. 1991, Nilsson & Brönmark 2000), and pike are known to select soft-rayed species, such as roach, over spiny-rayed species (Eklöv & Hamrin 1989, Amundsen *et al*. 2003).

Cannibalism was observed in relatively few cases in our study, despite the small size of the lakes, which is assumed to increase the likelihood of attacks on conspecifics (Craig 1996). Cannibalism in these lakes might be promoted by habitat competition, as it was mainly observed in mid-sized pike and targeted at relatively large-sized individuals (Raat 1988, Craig 1996, Anderson *et al*. 2007). However, we might have underestimated cannibalism, since our data were mainly collected in early spring and late summer, and cannibalism peaks shortly after hatching (Bry 1996). The low relative abundance of small size classes in the pike populations (Tiainen *et al*. 2017) could also indicate high, cannibalism-induced mortality in small individuals (Sharma & Borgstrøm 2008). Among the macroinvertebrate prey, *Asellus aquaticus* and *Ephemeroptera* larvae formed the highest contribution of the pike diet. Pike may have a higher capture rate when foraging on slow-moving benthic prey (Chapman & Mackay 1990), but this may also reduce the risk of cannibalism for small pike (Beaudoin *et al*. 1999). Invertivory may also be a resource partitioning strategy to avoid competition (Pedreschi *et al*. 2015).

Our hypothesis that the largest pike consume the largest prey was not fully supported by the results. The size of prey fish did increase as a function of pike size, but the largest prey size (as well as cannibalism) was observed in mid-sized pike (40–60 cm). This may be explained by differences in the habitat of large and mid-sized pike. The littoral zone in the study lakes harbours perch and large roach (Estlander *et al*. 2010), as well as small pike (Bry 1996), explaining the larger prey size and more frequent occurrence of perch in the diet of mid-sized pike. Large pike are more pelagial than smaller pike (Kobler *et al*. 2008, Pierce *et al*. 2013), but it might be more difficult in the pelagic habitat to forage on larger prey, as the pelagic zone of the study lakes is mainly inhabited by relatively small roach (Estlander *et al*. 2010). Roach also have better predation avoidance success in open water compared to perch, due to the longer escape distance (Ranåker *et al*. 2014). However, the number of large pike (>60 cm) with a non-empty stomach was quite low, increasing the uncertainty in the results.

The slow growth of pike in the study lakes also indicates a lack of optimum-sized prey (Margenau 1995). The average prey size in relation to pike size was lower (23%) than the 30% reported by Mittelbach & Persson (1998), but quite similar to the value of 19.5% observed by Margenau *et al*. (1995) from slow-growing pike populations in Minnesota. The observed importance of non-fish prey

(macroinvertebrates for smaller and amphibians and mammals for larger pike) also indicates resource limitation for pike in the study lakes (Tonn & Magnuson 1982, Rahel 1984, Rask *et al*. 1999). It additionally emphasizes the importance of the littoral zone for pike. In all the study lakes except Hokajärvi, macrophytes are concentrated along the narrow coastline, and, together with coarse woody debris (Harmon *et al*. 1986), create microhabitats for macroinvertebrates (Benke & Wallace 2003). Small humic lakes are closely connected to the terrestrial environment (Keskitalo & Eloranta 1999, Kankaala *et al*. 2010), which explains the occurrence of amphibians in pike diet. The shift in predation of large pike from fish to higher vertebrates might reduce their potential to control prey fish populations. However, the observed proportion of mammals and amphibians in the diet was generally low and they were consumed in a narrow time window (amphibians in early spring, mammals in late autumn). Thus, it seems unlikely that preying on higher vertebrates would reduce the effect of large pike on prey fish populations.

4.2. Pike trophic position according to SIA

Pike generally had more enriched $\delta^{15}N$ values from all studied trophic levels, indicating their top predator status in the study lakes (Paradis *et al*. 2008, Syväranta *et al*. 2010). However, the average $\delta^{15}N$ values were only 0.78 and 1.31‰ more enriched compared to the main prey species, perch and roach. Exclusive fish eaters should have values that are one trophic stage (on average 3.4‰, Post 2002) higher than their prey fish, but this was not the case. This indicates that a larger part of diet than suggested by SCA may consist of prey with a lower trophic position (Vander Zanden *et al*. (1997). However, the accumulation of $\delta^{15}N$ from a lower to a higher trophic status might vary from 2 to 5‰ (Post 2002), depending on the position in the ecosystem, and even small biases in estimates of $\delta^{15}N$ accumulation between trophic classes can lead to severe inaccuracies when evaluating the importance of prey items.

The observed increasing TP of pike as a function of length is probably a result of the diet including prey from a higher trophic level, i.e. fish (Venturelli & Tonn 1996). However, the TP was lower in pike that had been rapidly growing, even though feeding on highly energetic food, such as fish, should promote both growth and the TP (Diana 1996, Nyqvist *et al.* 2017). Possible explanations are restricted resources and the slow growth of large pike, which can elevate $\delta^{15}N$ values (Gannes *et al*. 1998, Gaye-Siessegger *et al*. 2007). Moreover, the slower metabolic rate of large and old individuals could increase $\delta^{15}N$ values, as has been found in walleye (Overman & Parrish 2001).

Contrary to our hypothesis, we observed a decrease in the TP of pike from 2008–2009 to 2013, after intensive harvesting of the pike populations in the study lakes. According to SCA, the proportion of fish in the diet was not higher in the latter sampling year, which could explain why the TP did not increase. A similar diet combined with the observed increase in the growth rate of pike (Tiainen *et al*. 2017) might explain the decrease in the TP, since we observed a lower TP in pike with a fast growth rate (Gannes *et al*. 1998, Gaye-Siessegger *et al*. 2007). The average

reduction in $\delta^{15}N$ values from 2008–2009 to 2013 was generally higher in pike than in perch or roach. Neither perch nor roach had a similar growth response to pike (unpublished results), which supports the decline in the TP as a function of increased growth. The decreases in $\delta^{15}N$ values in pike from 2008–2009 to 2013 were the highest in the smallest lakes (Majajärvi and Haukijärvi), where the nitrogen isotope value was below the that of perch in 2013. Majajärvi was the only study lake where intensive pike removal did not lead to an increase in pike growth (Tiainen *et al*. unpublished), despite having the highest density reduction (Tiainen *et al*. 2017). Therefore, the reduction in the $\delta^{15}N$ values is contradictory to what was discussed above regarding slow growth and a high TP in pike. A possible reason for the exceptionally low $\delta^{15}N$ values and lack of a growth response is that intensive fishing mainly removed active, fish-eating phenotypes, while a higher proportion of passive, invertivorous individuals remained in the population, even though our SCA results do not confirm this. In their novel study, Nyqvist *et al*. (2017) observed that slow-growing juvenile pike were less mobile and had lower $\delta^{15}N$ values than active and fast-growing conspecifics. In Haukijärvi in 2013, the $\delta^{15}N$ values of pike, perch and roach were similar. A possible reason for this is that in 2013, all three species fed on the same prey, because the lake was affected by flooding due to beaver (*Castor canadensis*) damming, increasing the availability of invertebrates (Nummi 1989).

The TP of pike clearly differed between lakes, being highest in Haarajärvi and lowest in Haukijärvi. This probably reflects the different trophic composition and morphology of the study lakes. Haarajärvi is the largest of the lakes and the only one with an oxygenated hypolimnion during summer stagnation. This increases the availability of suitable cooler water areas close to the feeding areas, which are crucial for large pike (Margenau *et al*. 1995, Pierce *et al*. 2013). According to the TP, pike prey on macroinvertebrates to a greater extent in Haukijärvi than in other lakes. Although invertivory is energetically ineffective and connected to slow growth (Venturelli & Tonn 2006), there are several possible reasons why it occurs even for relatively large pike (Beaudoin *et al*. 1999, Pedreschi *et al*. 2015). The low visibility may deter pike from finding optimal-sized prey (Rask *et al*. 1999). Interspecies competition and predation avoidance may also explain invertivory (Beaudoin *et al*. 1999), and the lack of suitable feeding and sheltering habitats in small humic lakes increases the impact of both factors. Large pike remained in the population despite the removal fishing in Haukijärvi (Tiainen *et al*. 2017), and the predation pressure on small pike remained. In lakes with limited habitats, strong competition will occur, and more aggressive and explorative genotypes may have a fitness advantage over more passive individuals due to gaining better territories and consuming energy-rich prey (Diana 1996). On the other hand, these advantages are gained at the expense of an increased risk of predation (Sih *et al*. 2004), especially when feeding in open water. In this context, feeding on slow-swimming invertebrates in a more complex environment represents an alternative "low risk–low reward" approach.

Carbon isotopes values in pike, roach and perch were generally closer to invertebrates than zooplankton, indicating an origin from littoral sources. The $\delta^{13}C$

values in pike were in most cases closer to roach than to perch, possibly indicating a higher share of roach in the diet, as supported by SCA. The pike $\delta^{13}C$ values differed between the study years only in Majajärvi, where the values decreased. This might indicate a general, fishing-induced shift in the pike population towards increased predation in the littoral area. The higher between-species differences in the $\delta^{13}C$ values after the pike fishing in the lakes might indicate better possibilities to inhabit different parts of the ecosystem after the decrease in pike control.

4.3. Correspondence between the trophic position determined by SIA and SCA

We observed a connection between SCA and SIA: invertivorous pike had a lower TP than exclusive fish eaters or individuals with empty stomach, as also found by Beaudoin *et al*. (1999). In contrast, Paradis *et al*. (2008) detected no differences in the TP between piscivorous and invertivorous individuals or individuals empty stomachs. The variation in the TP results reflected the diverse feeding behaviour of pike, which might explain the contradictory results (Paradis *et al*. 2008; Beaudoin *et al*. 1999). In general, SCA provides direct and specific information on the taxa ingested shortly before capture, while SIA represents the long-term diet (Beaudoin *et al*. 1999, Syväranta 2008). In our study, the increase in TP based on SIA and decrease in invertivory based on SCA in relation to pike length further supports the view that SCA can also provide information on the long-term diet. In addition, we found that individuals with empty stomachs had a relatively high TP, indicating that pike with empty stomachs are probably mainly piscivorous (Chapman *et al*. 1989, Paradis *et al*. 2008). In our study, more than half (51%) of pike had empty stomachs, which is typical for Esociformes (Arrington *et al*. 2002). The inability of MANOVA to detect significant between-lake, between-year or size-related differences in the pike diet emphasizes the problems with SCA for piscivorous species eating few, relatively large prey at a time.

4.4. The applicability of fin SIA for pike.

The fin SIA samples correlated significantly with the muscle SIA samples, showing that pike do not need to be sacrificed to obtain reliable SIA data. This is a significant advantage, especially when studying large pike, which are important for ecosystem functioning, and from a fisheries management point of view (Arlinghaus *et al*. 2010, Kuparinen *et al*. 2016). The observed high correlation between muscle and fin samples is in line with previous studies on other fish species (Jardine *et al*. 2011, Kelly *et al*. 2006, Sanderson *et al*. 2009). According to our results, the cleaning of fin samples reduces the difference between fin SIA and muscle SIA, especially in $\delta^{13}C$ values, and is thus recommended. The differences between fin SIA and muscle SIA can be corrected for using the equations presented in this study.

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PRIMARY RESEARCH PAPER

Intensive fishing can mediate stronger size-dependent maternal effect in pike (*Esox lucius*)

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Abstract In pike *E. lucius* L., evidence on maternal effect on reproductive output is mixed. We studied whether older and larger pike females produce eggs and larvae of higher quality (weight, starvation resistance) in three forest lakes in southern Finland. Later, the study lakes were subjected to intensive experimental pike fishing, which we assumed would increase resource availability and lead to higher maternal investment (larger egg size). Length of female pike was positively correlated with the dry weight of eggs and larvae but this relation was dependent on female age. In old females, the effect of female length on egg weight was lower or even negative. Survival analysis showed a positive effect of female length on larval survival time indicating that larvae from larger females are less vulnerable to starvation during the early stage of life. After the intensive pike fishing, the positive effect of female length on egg weight was stronger in all age classes probably due to the released resources. Based on the high quality and amount of reproductive products in large (but not very old) females, they are important for the reproduction of pike populations. This should be considered in fisheries management.

Keywords Pike · *Esox lucius* · Maternal effects · Egg · Larvae · Reproduction

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Introduction

Size-dependent reproductive traits have become a timely research subject due to fisheries-induced collapses in fish populations (Heyer et al., 2001; Hutchings & Reynolds, 2004). In many cases, size-selective fishing has led to decreased mean size of spawners and age of maturity (Sharpe & Hendry, 2009). It has been suggested that the size and age structure of the spawning population has great influence on reproductive capacity of fish populations (Scott et al., 1999; Venturelli et al., 2010), and, indeed, many heavily fished stocks have not been able to recover (Hutchings & Reynolds, 2004). This is suggested to result from declines in the average size of spawners and age of maturity (Olsen et al., 2005), resulting in lower

amount and quality of eggs and larvae (Trippel, 1995). Protecting the large individuals from fishing has been suggested as one solution to prevent this negative development (Birkeland & Dayton, 2005). Another option is balanced harvesting, in which ecosystem structure is retained by targeting a wide range of species and sizes in proportion to their productivity (Garcia et al., 2012).

A common feature of many large fish species is that larger and/or older females produce more and bigger offspring which have higher viability than small individuals (Chambers & Leggett, 1996; Einum & Fleming, 1999; Birkeland & Dayton, 2005; Johnston et al., 2007). Bigger larval size is strongly related to better survival (Perez & Munch, 2010), for instance because big larvae have more available food items (Mehner et al., 1998), less potential predators and better swimming performance after yolk sac period due to bigger yolk reserves (Ojanguren et al., 1996). Among piscivorous fishes (e.g. pike, *Esox lucius* L.) cannibalism is also an important factor amplifying alterations in survival between different-sized juveniles (Craig, 1996).

Pike is one of the core species and very important target species for fisheries in the temperate zone (Tonn et al., 1990; Craig, 1996). For the purpose of fisheries management, it is important to know how size and age affect offspring quality of pike. However, in pike the effect of female size and age on egg and larval characteristics seems to be ambiguous. Some studies have found a positive correlation between female size and egg diameter (Nikolsky, 1974; Wright & Shoesmith, 1988; Murry et al., 2008), and female size and early survival of larvae (Arlinghaus et al., 2010), while in other or even in the same studies egg dry weight or larval properties were not dependent on female size (Wright & Shoesmith, 1988; Murry et al., 2008). The influence of pike maternal age on egg and larval quality has been reported only in few studies (Nikolsky, 1974), although age is an important factor for the quality of reproductive products in several fish species (Berkeley et al., 2004; Kamler, 2005).

In this study, we focus on the relation between female characteristics (length, age) and the quality of reproductive products (egg dry weight, larval dry weight and starvation resistance) in three originally pristine pike populations. We also study the impacts of heavy exploitation on maternal effects in pike. We collected egg data before and after an experimental pike fishing project was conducted (2008 and 2012). Based on the previous studies (see above), we hypothesize that older and larger females produce larger eggs and larvae, the latter with better starvation resistance, even though these relations might not be very clear. We also assume that increased resource availability due to heavy exploitation leads to higher maternal investment (Edeline et al., 2007), larger egg size in this case.

Materials and methods

Study lakes

Pike were caught in 2008 and 2012 from three small, oligo-mesotrophic, humic and nearly pristine forest lakes in southern Finland (Estlander et al., 2010): Majajärvi (3.4 ha, 4.6 m), Hokajärvi (8.4 ha, 2.2 m) and Haarajärvi (13.8 ha, 6.1 m). Majajärvi has higher trophic status (average total phosphorus concentration in May–September 15 and 20 $\mu g\ l^{-1}$ in 2007 and 2011, the previous years before collecting the maternal data) than Hokajärvi (7 and 10 $\mu g\ l^{-1}$) and Haarajärvi (11 and 13 $\mu g\ l^{-1}$). The average temperature (May–September, 0.5 m depth) is higher in Majajärvi (16.6 and 17.7°C in 2007 and 2011) compared to the larger lakes Hokajärvi (15.8 and 16.8°C) and Haarajärvi (15.8 and 16.8°C). Other than research fishing has been prohibited in the lakes. The most abundant fish species in the lakes are perch (*Perca fluviatilis* L.), roach (*Rutilus rutilus* L.) and pike (Olin et al., 2010).

Measurements from adult pike

Altogether, 44 female (length 22.3–94.5 cm, age 3–19 years) pike were caught by ice fishing, fyke nets and wire traps between 3 weeks before and 2 weeks after the ice break in 2008 and 2012. The fishing gears were located extensively around the littoral in shallow (<3 m) water. Females were caught from three lakes: Haarajärvi (female $n = 14$ and 11 in 2008 and 2012), Hokajärvi ($n = 3$ and 7) and Majajärvi ($n = 9$ and 0). Additionally in 2008, 12 male pike of standard size (40.0–45.0 cm, 4–9 years) were collected for egg fertilization from two lakes Haarajärvi ($n = 6$) and Majajärvi ($n = 6$). In 2008, pike were killed before stripping of eggs and milt. In 2012, pike females were stripped and released ($n = 7$), or killed and frozen

before preparation of whole gonads ($n = 11$). All pike were measured for total length to the nearest mm. Age and growth were determined from *cleithrum*-bones with a linear model (Casselman, 1990) and from scales of the released individuals with a Fraser–Lee equation (Frost & Kipling, 1959) by one experienced reader. Back-calculated lengths were transformed to weights using lake- and year-specific length–weight relationships: $W = aL^b$, where a and b are constants calculated from a larger dataset from the study lakes ($n = 21$–59 per lake and year). Growth rate in the previous year before spawning (2007 or 2011) was calculated as $Gt = \ln(W_{t+1}W_t^{-1})$, where W_t is weight at age t.

Measurement of egg dry weight

From all females, randomly selected egg samples ($n = 25$–60 eggs) were taken for egg dry weight measurements. Oven-dried (24 h, 60°C) egg samples were weighted to the nearest 0.1 mg. Average dry weight was used as an indicator of egg quality, because it is tightly related to egg nutrient content and size of larvae (Ojanguren et al., 1996; Murry et al., 2008).

Fertilization and incubation of eggs

Experiments concerning fertilized eggs and larvae were conducted only in the year 2008. From females ($n = 16$, length 28.9–79.0 cm) that had sufficient amount of stripped eggs, randomly chosen sample (15–20 g, except two smaller samples of 9 g and 12 g) was taken for fertilization experiments. The eggs were dry-fertilized with milt (50 µl) of a standard-sized male (40–45 cm) from the same lake to control the possible influence of male size. The paternal effects in pike are largely unknown, but at least in salmonids and cyprinids males do not provide any chemical resources for the developing embryo (Pakkasmaa et al., 2001; Kamler, 2005), and thus the weight of the first hatched larvae should be independent of male characteristics. Eggs from Lake Hokajärvi were fertilized with milt of males from Lake Majajärvi as no males from Hokajärvi were available. Eggs of two females were fertilized with milt from one male to reduce possible paternal effects. For eggs from seven females this was not possible (not enough spawn-ready males from the same lake) and milt from one male per one female was used. After fertilization the eggs were incubated in sieve pails inside the hatchery of Evo Game and Fisheries Research Station. Water temperature was measured with automatic temperature loggers (HOBO Water Temp Pro) kept in the pails (average 12.4°C, range 11.8–15.1°C). The development of eggs was inspected twice a day and dead eggs were removed.

Hatched larvae and starvation experiment

From the first hatched larvae of every batch, two random samples (dry weight and starvation resistance) were taken. Only 13 females (length 28.9–79.0 cm) produced sufficient larvae ($n = 30$, except $n = 10$ for one sample) to measure larval dry weight (0.1 mg accuracy). Starvation resistance of larvae was tested to determine whether female length affects the survival time of larvae with sole yolk sac reserves. Larvae ($n = 44$–52) from 12 females (length 28.9–79.0 cm) were held in 2-l glass jars with sieved water (mesh size 25 µm), in the hatchery until the death of the last larvae. Dead larvae were counted and removed twice a day during experiment. The jars were aerated twice daily to keep oxygen content within 7–10 mg l^{-1}, and the jar locations were randomly mixed. Water temperature (range 7.9–14.1°C, average 10.9°C) was measured every 30 min with a temperature logger kept in a similar jar.

Statistical methods

The densities of pike populations (≥35 cm individuals) in the preceding year before collecting maternal data were estimated by the Petersen method as described in Kuparinen et al. (2012) (Table 1). According to Edeline et al. (2007), the energy gathered in the previous summer affects the next year's maternal investment in pike. Biomass estimates were based on Petersen estimates, the length–weight relationships (see above) and length distributions ($n = 26$–112 per lake and year).

The effects of female characteristics (length and age) on the dry weight of eggs and larvae were analysed with linear mixed models (*ln*-transformation was used to homogenize variation), where length and/or age were continuous variables, year was a factor and lake was a random variable. Quadratic and cubic effects of length and age were also analysed. The effect of year on the age-related growth rate of females

Table 1 Mark-recapture catches, estimated (95% CI) densities and biomasses of pike populations in the preceding years before collecting maternal data, and cumulative pike removal catch from 2008 to 2011

		Mark-recapture catch (*n*)	Recaptured (*n*)	Marked (*n*)	Density (*n* ha^{-1})	Biomass (kg ha^{-1})	Removal catch (kg ha^{-1})
Majajärvi	2007	17	11	42	19 (15–33)	15 (11–26)	19
	2011	14	5	37	22 (13–64)	15 (9–43)	
Hokajärvi	2007	70	17	58	11 (7–34)	8 (5–24)	12
	2011	15	6	37	13 (8–24)	6 (4–12)	
Haarajärvi	2007	46	15	44	17 (12–28)	10 (7–17)	9
	2011	75	36	148	19 (15–27)	12 (10–17)	

Density and biomass estimates are for ≥35 cm pike

was analysed with a linear mixed model including age as a continuous variable, year as a factor and lake as a random variable.

Survival analysis (Cox regression, SPSS 15.0) was conducted to determine whether female length has an effect on survival time of larvae with bare yolk sac reserves. Temperature sum (accumulated degree days above a threshold temperature of 0°C, Kotlyarevskaya, 1969) was used as the time variable, death of each larvae as status variable and female length as continuous covariate. Since the assumption of constant hazard ratio in Cox regression was not fulfilled, a time-dependent covariate (temperature sum × female length) was included in the model (Cox, 1972).

Results

The estimated pike densities and biomasses were highest in Majajärvi compared to Haarajärvi and Hokajärvi (Table 1). Pike fishing was the most intensive in Majajärvi and the least efficient in Haarajärvi. The removal did not decrease pike densities in any of the lakes, but the densities were a little bit higher in 2011 compared to 2007. Pike biomass remained the same in Majajärvi, decreased in Hokajärvi and increased in Haarajärvi.

The average egg dry weight ranged from 1.6 to 3.7 mg (mean = 2.5 mg, SD = 0.5). In the linear mixed model with female length as a single continuous explanatory variable, year as a class variable and lake as a random variable, a quadratic response in egg dry weight was observed (Table 2, Fig. 1). The heaviest eggs were observed from mid-sized females (peak at 62 cm), while the smallest and the largest individuals produced the lightest eggs. The effect of year was significant, and the eggs in year 2012 were heavier in relation to female length and the maximum weight of eggs was reached at a higher female length (3.4 mg at 90 cm) compared to year 2008 (2.3 mg at 48 cm). In the corresponding model with female age also the age had a quadratic effect and the heaviest eggs were produced by 9.3-year-old females but the coefficient of correlation was lower compared to the model with female length as a single variable (Table 2, Fig. 1). In the model, sampling year had no significant effect on the relationship between female age and egg dry weight and was reduced from the model.

In the model including both female length and age as continuous variables, the quadratic effect of both the continuous variables was insignificant. The effect of length on egg dry weight was different depending on the age (Table 2, Fig. 2). In young pike (<6 years), the effect of length on egg dry weight was always positive, whereas in older pike the effect of length was lower and even negative. Year had a significant effect and in 2008 the effect of length on egg dry weight was negative in older females (>5 years), whereas in 2012 the effect of length was positive in all ages and the heaviest eggs were produced by the youngest and largest individuals according to the model. In all the models, the cubic effects of female length or age were insignificant. The random factor lake did not have a significant effect in the above models.

The above changes in the relation between female size or age and egg dry weight can be related to the observed changes in the growth of sampled pike females. The back-calculated growth rate in 2011 (the previous year before collecting the latter egg samples) was higher than in 2007 both in Hokajärvi (0.48 and

Table 2 Modelled effects of female length and age as single variables and joint effects on egg dry weight

Variable	Estimate	SE	*P*	
Intercept	−6.192	2.728	0.029	$df = 43$
Ln length	3.261	1.366	0.030	$r^2 = 0.493$
Ln length * Ln length	−0.359	0.172	0.043	
Year (2008)	1.582	0.662	0.022	
Ln length * year (2008)	−0.464	0.172	0.011	
Intercept	−0.161	0.465	0.732	$df = 43$
Ln age	1.040	0.474	0.034	$r^2 = 0.129$
Ln age * Ln age	−0.247	0.118	0.043	
Intercept	−3.057	1.358	0.030	$df = 43$
Ln length	1.042	0.370	0.023	$r^2 = 0.494$
Ln age	1.231	0.597	0.046	
Year (2008)	1.607	0.675	0.023	
Ln length * Ln age	−0.309	0.148	0.044	
Ln length * year (2008)	−0.469	0.176	0.011	

Year was a class variable, except in the model of female age as a single variable where the effect of year was insignificant. Only the estimates for the first year (2008) are shown. Estimates of the last year (2012) were zero in the models

0.31, respectively) and in Haarajärvi (0.54 and 0.38). In Majajärvi, no ripe females were caught in 2012. Additionally, the growth rate of females in relation to their age was higher in 2011 than in 2007 (linear mixed model, year-effect, $P = 0.002$), and especially young females had increased their growth (linear mixed model, year * age interaction, $P = 0.006$). For example, the average growth rate of 6-year females was 0.37 in 2007 and 0.58 in 2011. In older pike the change in growth was lower. In the first year data, the females that produced the heaviest eggs were on average 9.3 years and 60.5 cm, whereas in the latter year the corresponding length at the age was 61.3 cm.

The average larval dry weight varied between 1.2 and 2.0 mg (mean = 1.7 mg, SD = 0.3). The dry weight of larvae had a significant positive correlation with female length, while the correlation with age was only near-significant (Table 3, Fig. 3). The effect of female age was not significant when included in the model with female length, nor was the interaction between length and age. When analysing the relation between eggs and larvae, the dry weight of larvae was significantly dependent on egg dry weight ($df = 12$, $r^2 = 0.335$, $P = 0.038$).

Starvation resistance of the first hatched larvae with bare yolk sac reserves ranged from 406 to 492° days (°C) (mean = 450° days). The Cox regression model estimated 50 and 90% mortality for larvae from median-sized (45.9 cm) females at degree days 359 and 439, respectively (Fig. 4). Starvation resistance had a significant positive correlation with female length (Table 4). Survival odds ratio increased 1.041 (95% CI 1.010–1.074) times for every 1-cm increment in female length, implying that, on average at a given temperature sum, a 10-cm-length increment in maternal size enhances survival probability of larvae by 41%. However, the relationship between female size and larval survival time varied with time as the effect of female length × time-dependent covariate was significant (Table 4). The model estimated that the larvae from the largest females survived longer and survival rates remained over 0.7 before a steep decrease after degree days 433 (Fig. 4). The larvae from the smallest female were estimated to die sooner and had survival rates lower than 0.7 already at a degree day 341.

Discussion

The results supported our hypothesis that the large pike females had better reproductive quality (heavier eggs and larvae) than the small ones. However, female age did not have a linear positive effect on egg weight as the oldest and largest females had rather low egg weight. Environmental conditions in the study lakes might explain the reduction of egg weight in the largest and oldest individuals. The lakes are small and of low productivity and especially large pike are growing quite slowly. It is possible that the largest individuals are not able to get enough energy to retain the quality of their reproductive products (Kamler,

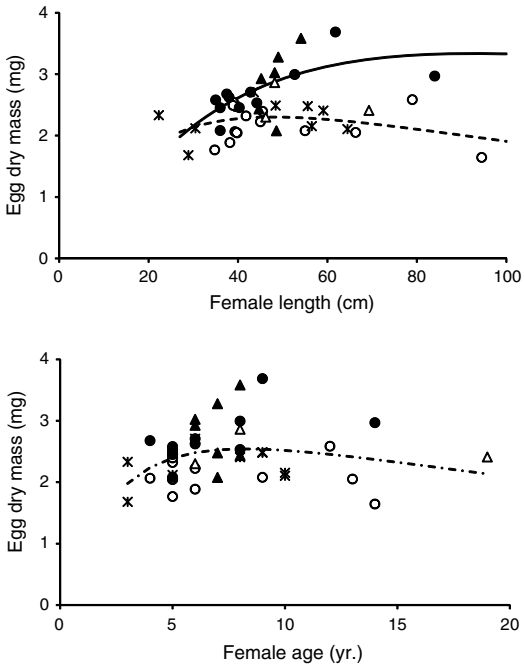

Fig. 1 Effect of pike female length (*above*) and age (*below*) on egg dry weight. *Symbols and colours* refer to different lakes and years: *white circle* = Haarajärvi 2008, *black circle* = Haarajärvi 2012, *white triangle* = Hokajärvi 2008, *black triangle* = Hokajärvi 2012, *asterisk* = Majajärvi 2008. *Curves* refer to model estimates for the year 2008 (*dashed*), 2012 (*solid*) and years combined (*dash dot*), see Table 1

2005; Edeline et al., 2007). We did not find any decrease in larval weight of the oldest and largest females, simply because we did not get enough larvae for measurements from these females. On the whole, the fact that we could find the decreased egg dry weight in the oldest females was only possible because the studied lakes have been prohibited from fishing, which enabled old individuals in the data. In other studies the degradation of egg quality may not have been detected because old individuals are missing due to high fishing mortality (Kamler, 2005). On the other hand, the dependence of the maternal effect on female age may partly explain why the correlation between maternal size and offspring quality has not been found in some studies (Wright & Shoesmith, 1988; Murry et al., 2008). To confirm this, more data have to be collected because age has been included as an explanatory factor only in few studies. Another subject needing more research is the relation between spawning time and egg size. Murry et al. (2008) found that the late-spawning pike produced heavier eggs than the early spawners, but we did not find any relationship between sampling date and egg weight despite the quite long period of data collection.

We found support for our second hypothesis that heavy exploitation can cause higher maternal investment. In 2012 compared to 2008, pike females produced much heavier eggs in relation to their size.

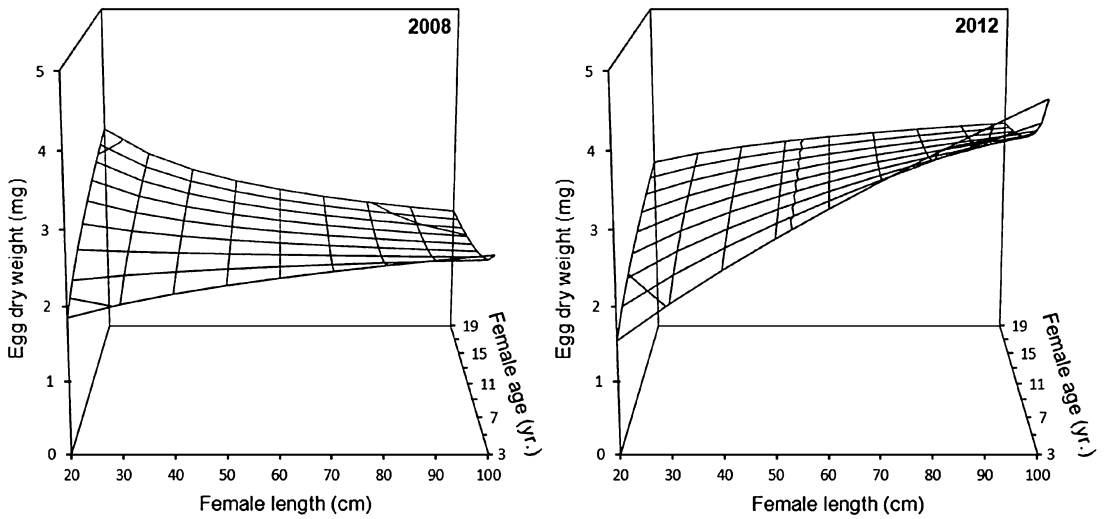

Fig. 2 Modelled effects (linear mixed model, Table 1) of pike female length and age on egg dry weight in 2008 (*left*) and 2012 (*right*)

Table 3 Modelled effects of female length and age as single variables on larval dry weight

Variable	Estimate	SE	*P*	
Intercept	−0.921	0.515	0.101	$df = 11$
Ln length	0.382	0.135	0.016	$r^2 = 0.422$
Intercept	0.141	0.192	0.479	$df = 11$
Ln age	0.215	0.103	0.060	$r^2 = 0.285$

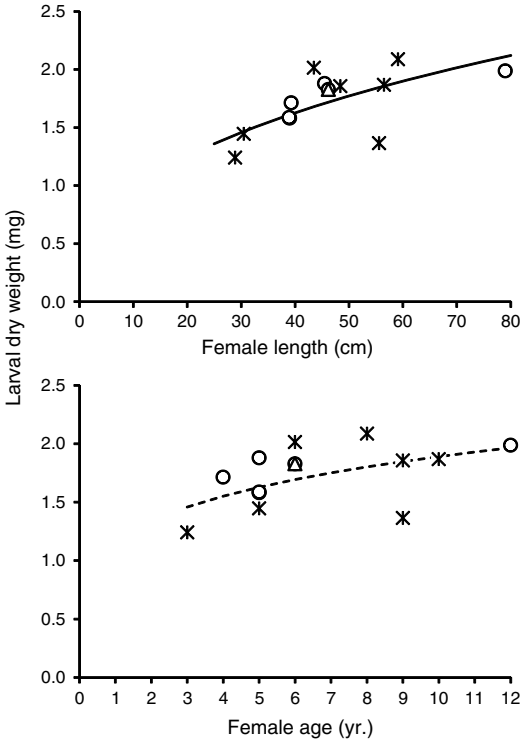

Fig. 3 Effect of pike female length (*above*) and age (*below*) on larval dry weight. *Symbols* refer to data of different lakes in 2008: *circle* = Haarajärvi, *triangle* = Hokajärvi and asterisk = Majajärvi. *Curves* refer to model estimates, see Table 2. The effect of age on larval dry weight is only near-significant ($P = 0.060$)

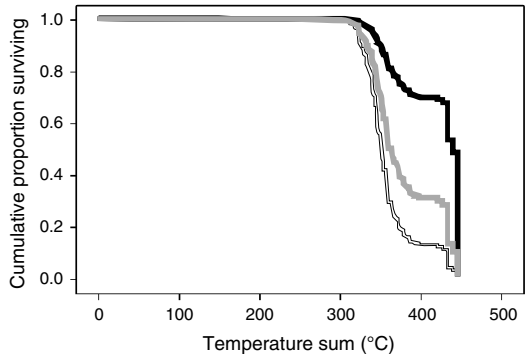

Fig. 4 Cumulative survival of pike larvae with yolk sac reserves according to Cox regression model. *White, grey* and *black* lines represent modelled survival curves of larvae from 29-, 46- and 79-cm females, respectively. The sizes of the females represent the minimum, median and maximum size of females that produced larvae for survival experiments

The released resources in consequence of heavy exploitation of pike stocks have probably enabled the observed higher investment to egg quality even though the estimated pike biomasses did not decrease notably or even slightly increase. The changes in trophic status and in water temperature were probably too low to cause such effect in maternal investment. Moreover, high water temperature might be harmful for pike in these lakes that have high humic concentration, strong thermal stratification and low oxygen levels in hypolimnion (Olin et al., 2010). Thus, the released resources were likely one mechanism that enabled the higher investment to reproduction, since especially young females had much higher growth rate in relation to length after the pike fishing. The change in the reproduction investment from 2008 to 2012 also supports the earlier assumption that the restricted resources are partly explaining the low egg weight in the oldest females. In Windermere (Edeline et al., 2007), pike had a tradeoff between growth and reproduction: gonad weight was lower in females with fast growth compared to slow growth. However, egg weight was not related to female growth. This was explained to be due to increased competition, since competition should favour large egg size (Roff, 1992; Robertsen et al., 2013). In the present study, both egg size in relation to female size and female growth rate increased after intensive fishing when competition was probably decreased. We were not able to observe fishing-related changes in total gonad weight, as most pike were caught during the spawning period when eggs run easily out.

Table 4 Cox regression survival analysis of newly hatched pike larvae with female length as a covariate

Variable	β	SE	Wald score	df	P	Exp(β) (CI 95%)
Female length	0.041	0.016	6.824	1	0.009	1.041 (1.010–1.074)
Female length × time-dependent covariate	<0.001	<0.000	25.376	1	<0.000	

β regression parameter, *SE* standard error for the regression parameter and *Exp(β)* Odds ratio i.e. change in the estimated survival probability for a unit increase in the predictor (female length). As the covariate effect of female length varied with time, a time-dependent covariate was included in the model

The observed relation between larval dry weight and female length is probably explained by the high energy reserves that big (and relatively young) females are able to invest in their eggs (Murry et al., 2008). Small differences in larval size might be accentuated in nature, due to intraspecific predation of pike by the same cohort (Grimm & Klinge, 1996). Even small differences in the larval size of pike may, therefore, have a high influence on the reproduction success of an individual. Larvae from large females also had better starvation capacity compared to larvae from small females. In consequence, almost all larvae from large females would survive even in very harsh environmental conditions. Swimming ability and energy reserves for food searching are probably correlated with starvation resistance, and in that case starvation resistance indicates viability even if starvation is not a probable threat. Unexpectedly, the maximum starvation capacity in this study was ca. twice long as compared to the value of ca. 200° days in other studies in similar temperatures (Kostomarova, 1959, 1961; Kotlyarevskaya, 1969). This distinction may be explained by differences in experimental circumstances, since egg dry weight and larval dry weight were quite close to the average values measured elsewhere: 2.0–2.5 mg for eggs (Desvilettes et al., 1997; Murry et al., 2008) and 1.7 mg for larvae (Desvilettes et al., 1997). Potential differences in genetic adaptation or in diet and nutrient content of pike populations might also explain the differences in larval starvation capacity. It also has to be noted that the selection on egg or larval size can be complex and have small-scale temporal and spatial variability, e.g. in areas of low intraspecific competition or in case of later emerging juveniles the advantage of large size may not be as evident (Robertsen et al., 2013).

In conclusion, the maternal effect on the reproductive products seems not to be as unambiguous in pike as it has been found to be in some other piscivores in temperate lakes, perch (Heyer et al., 2001; Olin et al., 2012) and walleye (*Sander vitreus* Mitchill) (Venturelli et al., 2010). Maternal size had positive effects on egg and larval quality except in the oldest slow-growing females. The highest dry weight of eggs and larvae in this study was achieved at a relatively high female age (9 years), which suggests that the best quality of eggs is probably achieved after several spawnings. Since the quality of reproductive products is not decreasing until females become very old, and as the amount of eggs is multifold in large females (Craig, 1996), large females are important for the reproduction of pike populations. This should be taken into account in fisheries management, e.g. when imposing size limits on fishing, as also stated in the simulation study of Arlinghaus et al. (2010).

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